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Spatial Aspects of Imprinting and Homing in Coho Salmon, *Oncorhynchus kisutch*

T. P. Quinn, E. L. Brannon, and A. H. Dittman

ABSTRACT: Analysis of seven years of coded wire tag data revealed that juvenile coho salmon, *Oncorhynchus kisutch*, released from two hatcheries in the Lake Washington watershed return almost exclusively to their hatcheries of origin. To determine if they learn the characteristics of more than one water source prior to seaward migration, coho salmon were reared in one of three hatcheries and were released from it or, after transportation, from a release site farther downriver. The locations to which adult salmon returned indicated that they had learned both the characteristics of their release site and the hatchery where they had been held prior to release. Salmon transported around much of their migratory route returned primarily to their release site, indicating that they needed to learn sequences of odors during their seaward migration in order to home in a complex river system.

The majority of salmonid fishes that survive to adulthood return to their natal site to spawn (Foerster 1936; Shapovalov and Taft 1954; Armstrong 1974; Swain 1982; Quinn and Fresh 1984; Berg and Berg 1987; Quinn and Tallman 1987; Quinn et al. 1987). The prevalence of homing in species with highly variable patterns of freshwater residence and anadromy (Rounsefell 1958) suggests that the process by which the fish learn the characteristics of their natal environment is flexible.

Coho salmon, *Oncorhynchus kisutch*, exposed to an artificial odorant prior to downstream migration as smolts are attracted to that odor at maturity (Scholz et al. 1976; Hasler and Scholz 1983). These and other results led Hasler and Scholz (1983) to hypothesize that salmon imprint only once, immediately prior to downstream migration. However, there is also evidence that wild coho salmon move considerable distances within watersheds before migrating to sea (Peterson 1982). Adult coho return to the site where they emerged from gravel nests as fry, not the site where they resided as smolts (Lister et al. 1981). Sockeye salmon, *O. nerka*, also typically home to tributaries of lakes experienced only as embryos or fry, not to the lake and its outlet experienced as smolts (see references in Quinn et al. 1987).

Transportation of juvenile salmon and trout within river systems has had mixed effects on homing. In some cases, fish captured during seaward migration, trucked to the lower Columbia River, and released, generally returned to the upriver rearing site (Ebel et al. 1973; Slatick et al. 1975). On the other hand, displacement from a hatchery to a release site downriver has often resulted in returns to the release site (Jensen and Duncan 1971; Vreeland et al. 1975; Cramer 1981; Vreeland and Wahle 1983).

It is thus unclear whether salmon learn the chemical characteristics of a single site at a specific developmental stage ("imprinting" by smolts: Hasler and Scholz (1983)) or if they learn a sequence of olfactory landmarks (Harden Jones 1968; Brannon 1982). By displacing smolts seaward, we can create gaps in their migratory experience as a way to examine the spatial aspects of olfactory learning. Specifically, we conducted two experiments in which salmon were released at their rearing sites or at a site downriver. The locations to which these salmon returned were compared among experimental groups and also compared to data from previous years on homing and straying within the watershed.

MATERIALS AND METHODS

Data Analysis on Homing in the Lake Washington Watershed

There are two major hatchery sources of coho salmon in the Lake Washington watershed (Fig. 1): the University of Washington's (UW) hatchery and the Washington State Department of Fisheries' hatchery on Issaquah Creek (Iss). We inspected the Washington Department of Fisheries and University of Washington data bases on coded wire tagged coho salmon and identified salmon recovered at these two hatcheries for return years 1979–85 to determine the extent of straying within this system.

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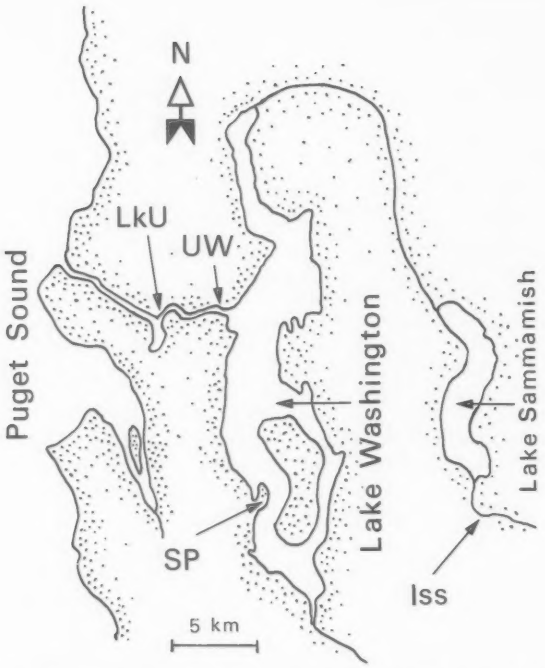

FIGURE 1.—Map of the Lake Washington watershed showing the locations of the release site on Lake Union (LkU) and the hatcheries at the University of Washington (UW), Seward Park (SP), and Issaquah Creek (Iss).

Treatment of Juveniles

In 1985 we initiated a study of patterns of imprinting and homing in the Lake Washington watershed. The basic experimental design was to expose coho salmon to the odors of Seward Park (SP) or Issaquah Creek (Iss) hatcheries and release them from those hatcheries or from a site 2.2 km downstream from the UW hatchery (Fig. 1). (The SP hatchery had been used for production of rainbow trout but not coho salmon prior to this experiment. Water for the SP hatchery is pumped from Lake Washington). Another group was reared in UW water and released at the downriver site.

Between 18 and 25 November 1985, adult coho salmon that had returned to the UW hatchery were spawned and the fertilized eggs incubated at the UW hatchery in dechlorinated city water. This is not the water source normally used in the hatchery; fish are normally incubated and reared in water pumped from the ship canal draining Lake Washington into Puget Sound (Fig. 1). The eggs hatched in January and yolk absorption was completed in March. In late March the fry were separated into three groups. Group 1, the control, was held at the UW hatchery and exposed to ship canal (UW) water during the smolt phase, from 20 May until 10–11 June, when the fish were tagged with internal coded wire tags. Fish in this study were judged to be smolts by their downstream migratory behavior and silvering. Only fish with silvery coloration and lacking parr marks were given coded wire tags. Group 1 fish were released into Lake Union, 2.2 km downstream from the UW hatchery, on 17 June. Groups 2 and 3 were transported to the SP hatchery on 21 March and reared there. They were tagged on 13 June (Group 2) and 14 June (Group 3). Group 2 fish were released into Lake Union on 1 July and Group 3 fish were released from SP on 27 June. Table 1 summarizes information on the treatments of the these groups.

On 19 March 1986 coho salmon at the Iss hatchery were marked by excision of the left or right ventral fin (10,000 fish per treatment). These salmon had emerged as fry in 1985 and smolted after one year in freshwater (average

TABLE 1.—Summary of coho salmon experimental treatments, indicating the date (in 1986) when fish were exposed to different water sources or moved. UW refers to UW hatchery water, CW refers to dechlorinated city water at the UW hatchery, SP refers to lake water at the Seward Park hatchery, Iss refers to the Issaquah Creek hatchery, and LkU refers to the Lake Union release site.

Developmental stage or operation		Experimental group				
		1	2	3	4	5
Eggs, alevins, and fry:	Site	CW	CW	CW	Iss	Iss
Parr:	Site	CW	SP	SP	Iss	Iss
	Date	—	3/21	3/21	—	—
Smolts:	Site	UW	SP	SP	Iss	Iss
	Date	5/20	—	—	—	—
Tagging:	Site	UW	SP	SP	Iss	Iss
	Date	6/10–11	6/13	6/14	3/19	3/19
Release:	Site	LkU	LkU	SP	LkU	Iss
	Date	6/17	7/1	6/27	3/19	4/9
	Size	10.0 g	12.6 g	11.3 g	26 g	26 g
	Number	8,491	10,020	10,148	10,000	10,000

weight = 26 g), unlike the UW coho, which smolted in their first spring. Those with their right fin clipped (Group 4) were trucked in two groups of 5,000 fish each to the Lake Union site and were released on 19 March. Those with the left ventral fin clipped (Group 5) were returned to the hatchery pond and released from the hatchery with the normal production fish on 9 April.

Recovery of Returning Adults

It was anticipated that most experimental coho escaping the fisheries would return to the hatcheries at UW, SP, or Iss, primarily in 1987. Coho salmon of the UW population almost all return in the second fall after their release (Brannon et al. 1982) and few precocious males ("jacks") occur. A trap to recover salmon returning to the SP hatchery was built in summer 1987; therefore no jack (1986) returns would have been collected that year, but the UW and Iss hatcheries were operating in 1986 to collect jacks. All hatcheries were also open in 1988 for salmon returning in the third fall after release. In addition to these primary recovery sites, the National Marine Fisheries Service (NMFS) operates a small hatchery on the opposite side of the ship canal. While no salmon released from NMFS were expected to return in 1987, the hatchery trap was operating and salmon entering it were checked. Some salmon released in Lake Union (where there is no hatchery or spawning ground) might have been expected to enter the NMFS facility if they had not imprinted on the UW hatchery.

RESULTS

Analysis of the historical data revealed that from 1979 to 1985, 5,465 coho salmon with coded wire tags from UW and Iss were recovered at these two hatcheries. Of 4,696 tagged UW coho salmon recovered, only two (0.04%) strayed to Iss. Similarly, of 769 tagged Iss coho, only one (0.13%) entered the UW hatchery. Thus, virtually no straying takes place between these two hatcheries when coho are reared and released at the hatcheries.

Only one jack from the UW-SP transfer groups (from Group 2) was recovered in 1986 at the UW hatchery, indicating that the absence of a return trap at SP did not bias the data significantly (Table 2). Group 1, exposed to UW water and released into Lake Union, returned exclusively to the UW hatchery (34/34). Group 2, which had not directly experienced UW water but had been reared at SP and released into Lake Union returned primarily to the UW hatchery (Table 2) but seven salmon were recovered at SP. Group 3 fish, reared in the same manner as Group 2 fish but released from SP, returned exclusively to SP.

In 1986 and 1987, 73 fish with clipped ventral fins were recovered at the UW and Iss hatcheries. Group 5, reared and released from Iss

TABLE 2.—Patterns of homing displayed by adult coho salmon from different experimental rearing regimes. Numbers listed represent actual fish returning while numbers in parentheses are the percentage of each experimental group returning to that recovery hatchery. Groups 3 and 5 were reared and released at Seward Park and Issaquah Creek hatcheries, respectively. Groups 1, 2, and 4 were released into Lake Union but had been reared at the University of Washington, Seward Park, and Issaquah Creek hatcheries, respectively.

Recovery hatchery	Experimental group				
	1	2	3	4	5
U. of Washington	34(100)	44(86)	0	15(88)	2(4)
Seward Park	0	7(14)	44(100)	0	0
Issaquah Creek	0	0	0	2(12)	54(96)

hatchery, generally returned to Issaquah Creek (54/56 recoveries). The return of transported fish (Group 4) was lower but they tended to enter the UW hatchery (15/17 recoveries). Fifteen coho salmon entered the NMFS facility in 1987 but none were from any of the experimental treatments.

DISCUSSION

The coded wire tagging data demonstrated that salmon home almost without fail to the UW and Iss hatcheries if they have been reared and released at these sites. The return of all members of Group 1 to the UW hatchery supported the findings of many previous studies (reviewed by Hasler and Scholz (1983)) that exposure to a water source at the smolt stage or at the time of release provides a sufficient basis for homing. Similarly, Group 3, released from SP, returned exclusively to SP. Fish from Group 2 had experienced a gap in their migration, relative to Group 3. They were reared at SP during the parr and smolt stages but did not experience the route from SP to the Lake Union release site, a distance of some 18 km. Most of these fish entered the UW hatchery but 7 of 51 returned to SP.

The Iss controls (Group 5) returned to that hatchery and the salmon trucked to Lake Union tended to enter the UW hatchery, though the return rate of the experimentals was quite low. The salmon held in Iss hatchery before being trucked to Lake Union presumably learned the characteristics of their hatchery but were unable to detect them when they returned to Lake Union as adults. Taken together, the results of the experiments support Harden Jones' (1968) hypothesis that salmon learn and subsequently retrace a sequence of odors. In situations where the home odor travels relatively undiluted or unchanged downriver, salmon artificially displaced downriver might be able to home successfully. However, if the home water is diluted or altered by passage through lakes (as may have occurred in our experiments), salmon may only return as far as their release site.

It is possible that the differences between the patterns of homing displayed by Groups 2 and 3 and Groups 4 and 5 could be due to differences in the degree of smolting. For example, if there is a very tight window for imprinting which is linked to some subtle (or unknown) changes during smoltification, then perhaps 7 of the 51 returning fish from Group 2 had reached and ended the imprinting phase prior to transport to Lake Union. This would imply that all the returning fish were able to detect SP water but that only the above 7 responded to it. This explanation seems unlikely, however, since these fish were released during a relatively late phase of the smolting process. If imprinting is linked to events such as natural thyroid hormone peaks and the onset of silvering and downstream migration (Hasler and Scholz 1983), then all the fish in Group 2, whether released at SP or transported to Lake Union, would have been expected to return to SP.

The gap in experience that we provided was relatively short in distance but great in effect on homing, compared with experiments on the Columbia River (e.g., Slatick et al. 1975) in which much longer displacements did not affect homing. However, extreme treatments, such as displacement 574 km downriver from Dworshak Hatchery to Bonneville Dam (Slatick et al. 1982), did impair homing. Presumably, if salmon can detect the upriver odor when they arrive at the release site, little effect of displacement will be recorded, regardless of the linear distance.

The fish displaced downriver to Lake Union as smolts tended to enter the UW hatchery even though they had not experienced its water. We hypothesize that these fish initially returned to the release site in Lake Union and found it unsuitable for spawning. The salmon could then have been attracted to the odors of the 1,708 adult coho salmon which were in the UW hatchery over the course of the season. By comparison, the equally proximate NMFS facility contained only 15 adult coho. Adult coho salmon can recognize waters conditioned by conspecifics (Dizon et al. 1973) and behavioral attraction to such species-specific odors has been documented

(Quinn et al. 1983). The return of Group 2 to Seward Park can be explained only by the fact that the salmon had been reared there. Iss hatchery produced about 12 times as many coho salmon as the UW hatchery in 1987, but no fish from Group 2 entered Iss, indicating that little wandering took place.

The patterns of freshwater residence and seaward migration vary greatly among and within salmonid species, yet homing to the natal site prevails throughout the family. There seems to be a flexible system by which site-specific odors are learned prior to and during seaward migration. Hasler and Scholz (1983) demonstrated a link between the thyroid hormones associated with smolt transformation (Dickhoff et al. 1978; Dickhoff and Sullivan 1987) and olfactory imprinting. However, the ability of salmon to learn odors on more than one occasion is not fully compatible with a single peak of thyroid hormones in spring. The solution to this problem may lie in the discovery by Dickhoff et al. (1982) that exposure of coho salmon to novel water sources at the time of year when they would migrate to sea induces transient peaks in thyroid hormone levels. Thus, if thyroid hormones are linked to olfactory learning, there may be feedback from migration to hormones, resulting in additional learning during migration. Exposure to novel waters (e.g., at the confluence of rivers) might induce elevated hormone levels and trigger learning of the water source as an olfactory way-point to be used during upstream migration years later.

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Spatial Distribution of Juvenile Salmonids in the Hanford Reach, Columbia River

Dennis D. Dauble, Thomas L. Page, and R. William Hanf, Jr.

ABSTRACT: The cross-sectional distribution of juvenile chinook salmon, sockeye salmon, and steelhead was determined in the Hanford Reach of the Columbia River from July to September 1983 and from April to July 1984. Fish were sampled with fyke nets from anchored barges, movable shoreline fyke nets, seines, and with electroshocking equipment. Fall chinook salmon from naturally spawning populations and from hatchery releases were the principal species collected in the spring. Zero-age fall chinook salmon occurred primarily in shoreline areas of reduced current velocity but were present throughout the river cross section during their early rearing and outmigration period. Hatchery-released fall chinook smolts were less abundant in nearshore areas than were wild fish. Yearling spring chinook salmon, sockeye salmon, and steelhead smolts from upriver areas were collected mainly from the bottom, midchannel zone of the river. Principal downstream movement of all species occurred from 2200 to 0400 [PDT]. Fish collections followed an activity pattern that included migration, feeding, and resting periods.

Knowledge of the distribution of migrating fish is important both to fisheries managers and to scientists interested in migratory behavior. From a practical standpoint, knowledge of where fish migrate may allow technology to be developed with minimal impact on that resource. Information on the location of fish during different phases of their life cycle may also provide clues to specific environmental factors that influence their behavior and ultimately affect their survival (Coutant 1986). Migrational characteristics are adapted toward particular life history strategies (Smith 1985); therefore, comparisons of distribution among species or size classes can further our understanding of anadromous fish biology.

Information on the spatial distribution of juvenile salmonid outmigrants in nonimpounded waters of the mainstem Columbia River is limited to studies of 0–age fall chinook salmon, *Oncorhynchus tshawytscha*, by Mains and Smith (1964). Investigations of the distribution of migrating salmonids in other river systems have been directed at determining the behavior of juveniles during movement from spawning or nursery areas. For example, in the Skeena River drainage in Canada, the lateral distribution of outmigrant pink salmon, *O. gorbuscha*, and sockeye salmon, *O. nerka*, was positively correlated with current velocity. In contrast, coho, *O. kisutch*, and chum, *O. keta*, salmon fry were more uniformly distributed across the river (McDonald 1960). Studies with juvenile sockeye salmon in the Newhalen River, AK showed that most fry and smolts were present in the faster midchannel areas and near the surface (Dames and Moore 1982). To our knowledge, no studies have been conducted to quantify and compare the cross-sectional distribution of juvenile salmonids in lotic environments.

Descriptions of habitat selection have been conducted for many salmonid species in small stream systems. Most indicate a general relationship between increased fish size and greater water depth and/or current velocity (Hartman et al. 1967; Lister and Genoe 1970; Everest and Chapman 1972; Wankowski and Thorpe 1979). Whether this relationship applies to the spatial distribution of migrating fish in a large river has not been established.

We report results from field studies conducted in the Hanford Reach of the mid-Columbia River in 1983 and 1984. The Hanford Reach is now the only unimpounded section of the mainstem Columbia River above Bonneville Dam and below the international border (Fig. 1). Our objective was to obtain estimates of the relative cross-sectional distribution of juvenile chinook salmon, sockeye salmon, and steelhead, *O. mykiss*, during their spring and summer outmigration from upriver spawning and nursery areas. These estimates of distribution were needed to assess the potential for fish to pass through a midriver thermal discharge, located downstream from the study site. Capture locations of fish were also

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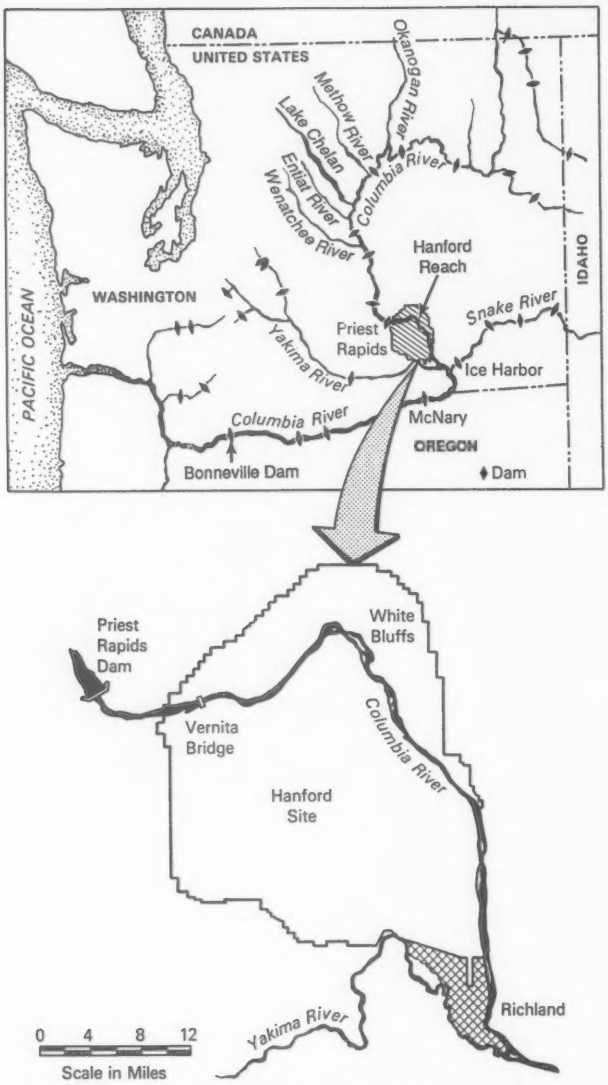

FIGURE 1.—Location of the study area in southeastern Washington.

described in relation to bathymetric and hydrologic characteristics of the river.

STUDY AREA

The Columbia River is about 330 m wide at the study site (river km 613) with average flows of 3,400 m^3/s. The channel is straight, and there are no islands or other major changes in the channel configuration within 6 km of the site. The river bottom slopes gradually from the Benton County side of the river to a distinct channel and rises steeply to the opposite shoreline (Fig. 2). Bottom substrate consists primarily of packed cobble, >10 cm in diameter, and boulders.

River flows in the Hanford Reach are controlled by releases at upriver dams in response to hydroelectric power demand and fish passage requirements. Seasonal flows at the site ranged from 1,220 to 5,270 m^3/s in the summer of 1983 and from 2,600 to 6,330 m^3/s in the spring of 1984. River depths varied by about 4 m as a

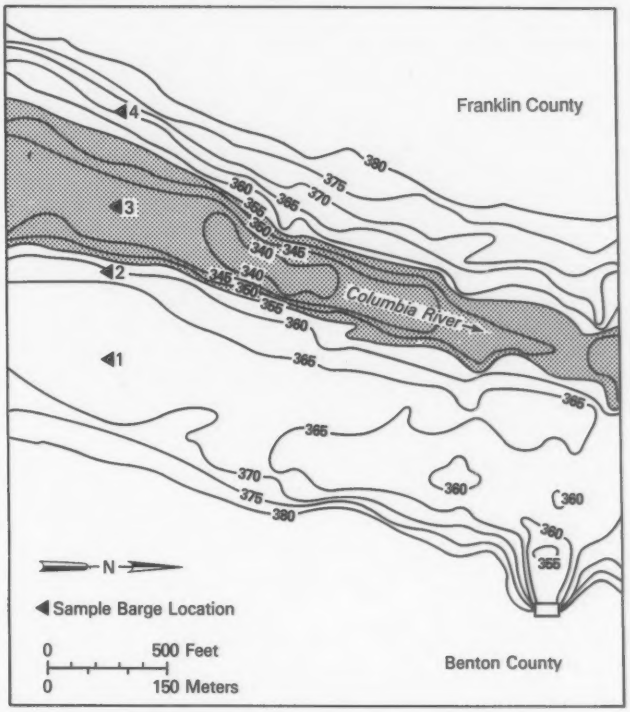

FIGURE 2.—Bathymetry of the Columbia River near the study site, and relative position of barge sampling stations. Contour intervals are river level elevations in feet. The stippled portion shows the midchannel region.

result of this flow pattern. Velocities across the river depended on location, station depth, and river stage (Table 1). Maximum velocities occurred near the river surface. Velocities at midchannel ranged from 0.6 to 2.6 m/s and velocities near the shoreline ranged from 0.1 to 0.5 m/s.

Water temperatures ranged from 18.0°C in August 1983 to 5.2°C in April 1984. Temperatures were uniform across the river until late May; however, from late May through September, daytime water temperatures differed by 2° to 3°C between nearshore and midstream areas because of solar radiation. Visibility (Secchi disc depth) ranged from 142 to 440 cm. Visibility was at a minimum during the late spring freshet and at a maximum in September.

TABLE 1.—Mean river depth and current velocities at the fyke net sample positions during spring 1984 studies.

Station	Mean depth (m)	Net position	Mean water velocity (m/s)
Barge 1	5.5	Surface	0.79
		Middepth	0.67
		Bottom	0.37
Barge 2	6.5	Surface	1.25
		Middepth	1.16
		Bottom	0.98
Barge 3	12.1	Surface	1.59
		Middepth	1.43
		Bottom	1.28
Barge 4	5.9	Surface	0.98
		Middepth	0.79
		Bottom	0.24
Shoreline 1[1]	1.5	Surface	0.18
Shoreline 2[2]	1.6	Surface	0.37

[1]Benton County shoreline.
[2]Grant County shoreline.

METHODS

Several types of gear were used to provide estimates of fish distribution. Offshore fyke nets mounted on stationary barges were the principal

collection method because the nets could be simultaneously used at different depths and locations. In 1984, fyke nets were also used near the shoreline to provide comparisons of nearshore abundance. These nets could be moved to accommodate daily fluctuations in river flow. Boat electroshocking and beach seining were also used to monitor nearshore abundance of juvenile salmonids.

Fyke Net Systems

Four steel barges were used as fishing platforms for the offshore fyke nets (barges 1, 2, 3, and 4; see Figure 2). Two barges were permanently anchored at opposite shorelines, one in midstream, and the other in midchannel. The dimensions of the two barges were 4.3 by 8.1 m and two were 4.9 by 9.1 m. The platforms and rigging setup were modified after Mains and Smith (1964). A 13 mm (½-in.) steel cable was used to attach each barge to a 4,500 kg steel anchor (Fig. 3). A drum winch, with a 6 or 8 mm windlass cable, was used to raise and lower the net from the back of the barge. Battery-powered windlass winches (Superwinch, Model EW 600[1]) and hydraulic-powered gypsy hoists (Kolstrand Model 5-24) were used to operate the drum winch on the two shoreline and two midstream stations, respectively. Hand hoists (come-alongs) were used to maintain tension on the windlass cables because the river levels fluctuated daily.

Each barge fyke net had a 1.5 × 1.5 m opening and was 7 m long. The main body tapered uniformly to a 20 cm diameter opening at the cod end. All netting was made of 6 mm (¼ in.), heavy-duty, knotless nylon mesh. The net frame was built from streamlined aircraft tubing, measuring 86 × 36 × 1 mm. A General Oceanics Model 2030 flowmeter was attached to the mouth of the net. In 1984, a detachable net constructed of 5 mm (3/16 in.) heavy-duty, knotless nylon mesh was attached to the nylon sleeve on the cod end to retain smaller fish. This net was 1 m long, 20 cm across, and had a zippered opening for reaching fish and removing debris.

Shoreline fyke nets had a 1 m^2 opening and were 4.5 m long. No wings were used, but an internal fyke was added that decreased the effective mouth size to 0.3 m^2. All netting was made of 5 mm (3/16 in.), heavy-duty, knotless nylon mesh. The mouth or upstream end of the net was rigged with a weight/float line to keep it vertical. A weight/float retrieval line was also attached to the downstream end of the net.

Fyke Net Sampling Design and Procedure

The offshore nets were fished from each of the four barges for five 24 h periods each week from 26 July through 24 September 1983 and from 23 April to 29 June 1984. We also sampled for four days in late July 1984. The spring sampling coincided with the expected maximum abundance of

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

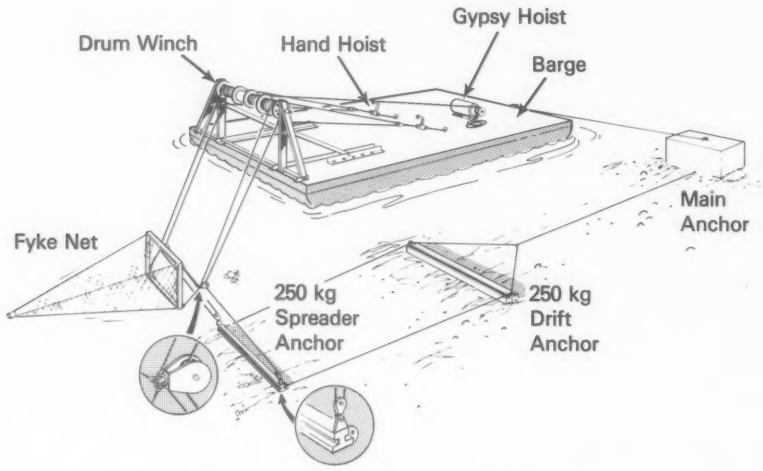

FIGURE 3.—Design of the fyke net rigging and anchoring system.

juvenile fall chinook salmon emerging from the Vernita Bar area (Page et al. 1976) and with the period of greatest catches of juvenile coho, chinook, and sockeye salmon, and steelhead at Priest Rapids Dam (Becker 1985). The late summer sampling corresponded to the period of greatest catches of 0–age fall chinook salmon at Priest Rapids Dam (Raymond 1967; Sims and Miller 1977; Hovland et al. 1982).

Sampling periods within each week were selected by a stratified random process to give equal weight to weekday and weekend intervals. To differentiate between diel variations in migration pattern, each day was divided into four equal time blocks starting at 0400 PDT (i.e., 0400–1000, 1000–1600, 1600–2200, and 2200–0400). The scheme provided one all-dark, one all-light, and two transition (dawn and dusk) periods. All barge stations were fished simultaneously at a predetermined depth. One net set of approximately 2 h duration was taken at each of the surface, mid-, and bottom depths according to a random schedule during each 6 h time block. Water temperature, sample and station depths, duration of set, and flowmeter readings were recorded for each sample. Secchi disc depth was recorded daily at noon. Current velocity measurements were taken at 1 m below the surface, at middepth, at 1 m from the bottom at each of the four stations, and over a range of flows using a Bendix Model Q-15 current meter.

Three people worked each shift. Generally, a net could be raised, checked for catches, cleaned of debris, and lowered to the next sampling depth within 5 minutes. Nets at all four stations would usually be tended and repositioned within 15 to 30 minutes. Some samples were lost because of water levels and high flows. Once, a submerged log hit the midchannel net and broke the spreader anchor cable.

The shoreline fyke nets were used for five 24 h periods each week from 30 April to 29 July 1984. To differentiate between diel variations in catch, each 24 h day was divided into four equal time blocks of 6 hours each. Collection intervals coincided with the four barge fyke net sampling periods. Nets were set parallel to the shoreline and opposite the barges at depths of 1 to 2 m.

Supplemental Sampling Gear

A boat-mounted electroshocker (Smith-Root Type VI Electrofisher), powered by a 240 volt generator, was used to sample nearshore fish populations near the barge stations during 1983 and 1984. Each shoreline station was sampled once per week during each of the four 6 h time blocks when fyke nets were sampled. A single pass with the electroshocker was conducted through each 400 m transect at depths of 1 to 2 m. Stunned fish were collected with dip nets, and all juvenile salmonids were measured and released. Catch per unit effort was based on duration of shock.

Duplicate seine hauls were made at each of four permanent stations near the barges with a 9.1 by 1.2 m net constructed of 3 mm (⅛ in.), heavy-duty, knotless nylon mesh. The stations were sampled once per week during daylight hours from April through June 1984. About 50 m^2 of shoreline were sampled with each set. All salmonids were enumerated and subsamples (usually five fish per station) were retained for measurements.

Data Analysis

Estimates of the proportional distribution of fish groups caught at various stations and depths by fyke net were based on a multinomial distribution of the fish caught among the various combinations of station and depth (Cochran 1977). Relative catch per unit effort (CPUE) was calculated on the basis of unit time/cross-sectional area sampled and on volume sampled. A log-linear model was developed to evaluate proportional distribution estimates of 0-age fall chinook, spring chinook, and sockeye salmon smolts using the CATMOD procedure in SAS (SAS 1985). The model was then used to test for two-way interactions among fish groups, barge location, and sample depths. A binomial test for differences (Mainland et al. 1956) was also used to evaluate patterns of distribution for some species.

RESULTS

Estimates of cross-sectional distribution were different for each of the six groups of juvenile salmonids collected. The differences are described in terms of species, life stage, and migration timing.

Distribution of 0-Age Chinook Salmon

Three groups of 0–age chinook salmon were collected: 1) naturally produced (wild) fish originating from adults spawning in the Hanford Reach above the study site, 2) hatchery fish

from the Priest Rapids Dam rearing facility, and 3) late summer migrant fish from wild stocks that spawn above Priest Rapids Dam or from hatchery releases at Wells Dam. Peak abundance of these three groups occurred at different times (Fig. 4). Juvenile fall chinook salmon originating from the Hanford Reach were collected in higher numbers than any other salmonid group. These fish were already present in the river when sampling began in late April

Spring Outmigration

Wild and hatchery 0–age chinook salmon occurred throughout the river cross section at Hanford, but the highest concentrations occurred at nearshore barge stations (Fig. 5). About 45% of the fish (n = 6,281) were collected at barge 4. In contrast, only 7% of the 0–age chinook salmon were collected in the shoreline nets.

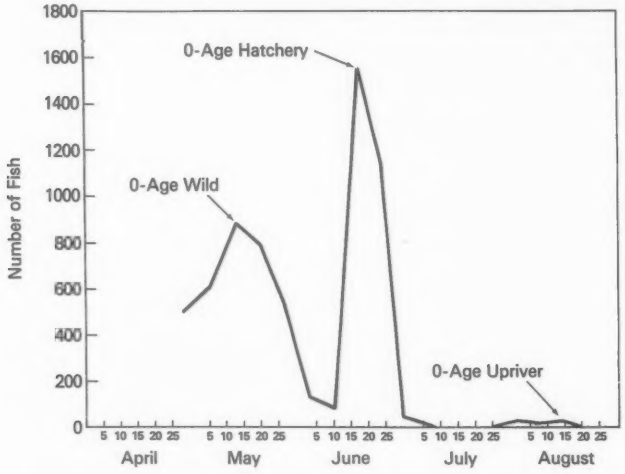

FIGURE 4.—Seasonal patterns of abundance for 0-age chinook salmon populations captured by fyke net near the study site. Sampling effort was uniform throughout the collection period.

1984. Populations peaked in late May, and small numbers were still present in late June when sampling ended. About 60% of the 0–age fall chinook salmon collected in 1984 were wild fish that originated from the Hanford Reach. Hatchery-reared fish appeared in nets within 24 hours of their release from the Priest Rapids rearing facility. These fish differed from wild salmon because of their larger size and deeper body. Most salmonids collected during June were hatchery-released fish. Small numbers of 0-age summer or fall chinook salmon were also collected from July to September 1983 and in July 1984. These fish probably originated in the Wenatchee River, with lesser contributions from the Entiat, Methow, and Okanogan Rivers. Only limited spawning of fall and/or summer chinook salmon occurs in the mainstem Columbia River above Priest Rapids Dam (Horner and Bjornn 1981).

TABLE 2.—Summary of average catch per unit effort for 0-age chinook salmon caught by fyke nets in spring 1984.

Station	Depth	Number/h	Number/$m^3 \times 10^6$
Shoreline 1[1]	Surface	0.3	669.0
Barge 1	Surface	0.4	50.7
	Middepth	0.9	120.8
	Bottom	1.3	199.9
Barge 2	Surface	0.6	50.7
	Middepth	0.4	36.4
	Bottom	0.9	88.6
Barge 3	Surface	1.4	90.4
	Middepth	0.5	33.6
	Bottom	2.2	164.6
Barge 4	Surface	1.7	230.5
	Middepth	2.0	285.7
	Bottom	3.5	829.6
Shoreline 2[2]	Surface	0.2	975.0

[1]Benton County shoreline.
[2]Grant County shoreline.

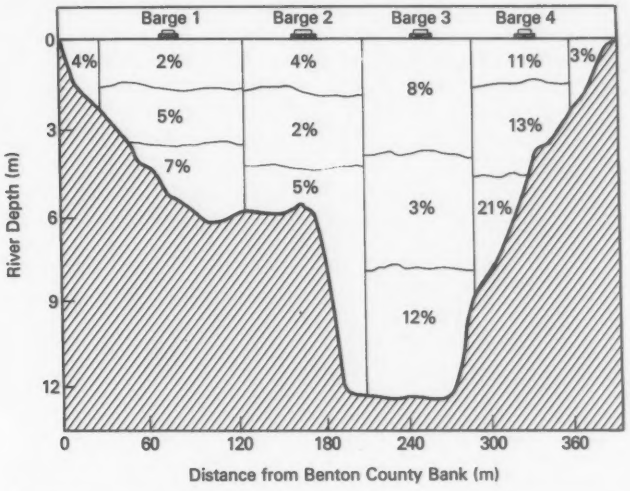

FIGURE 5.—Cross-sectional distribution of 0-age fall chinook salmon (n = 6,281) caught in shoreline and barge fyke nets during spring 1984. Note: horizontal scale is reduced.

Overall, fyke net catches of 0–age chinook salmon ranged from an average of 0.3 fish/h at the Benton County shoreline (shoreline 1), to 3.5 fish/h at barge 4 (Table 2). A peak catch of 152.8 fish/h occurred on June 14 from the bottom depth at barge 4. This quantity corresponded to 5.6 fish/100 m^3 of water filtered through the net. Based on water volume, catch per unit effort was greatest at the Grant County shoreline (shoreline 2).

Little change in fish size was noted for 0–age chinook salmon collected with fyke nets in April and May; 80 to 90% of the fish collected were ≤45 mm fork length (FL) (Fig. 6). However, in June the 0–age chinook salmon collected in the shoreline nets were smaller than those collected in the barge nets. In June, the barge nets collected mainly hatchery fish >80 mm FL, while 60% of the shoreline net totals were wild fish <70 mm FL.

The relative proportion of 0–age chinook salmon caught at the various fyke net stations

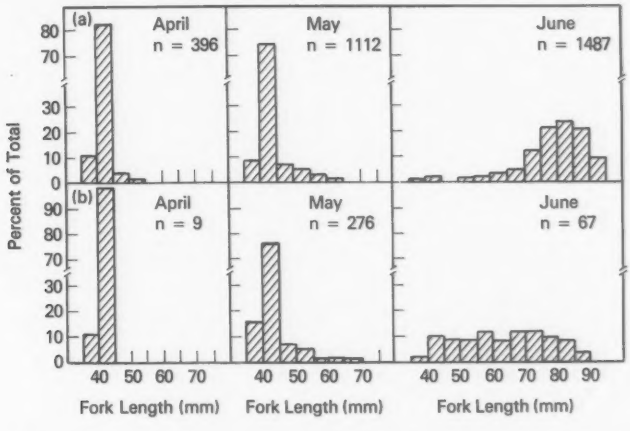

FIGURE 6.—Length-frequency of 0-age fall chinook salmon collected with fyke nets: a) barge sets and b) shoreline sets.

varied seasonally. In general, fish caught in April and May (all wild fish) occurred to a greater extent in shoreline areas where currents were reduced than fish caught in June (~90% hatchery fish). Nearly three times as many 0-age salmon were collected from the two midstream stations (barges 2 and 3) in June than in April and May (Table 3). Analysis of the number of fish caught showed a highly significant interaction ($P \leq 0.0001$) between the April/May and June groups and capture location (barge or depth).

Late-Summer Outmigrants

Low numbers of juvenile fall and summer chinook salmon occurred at Hanford during late summer (July to September). We captured most of these fish (21 of 26) in the midchannel station (barge 3), and 68% of them were collected from the bottom sets. CPUE at barge 3 was 2.2 fish/100 h of sampling (all depths combined). This corresponded to only 1.6 fish/$m^3 \times 10^6$ of water filtered through the nets. CPUE at barge 3 during the peak sampling interval (early August 1983) was 7.1 fish/100 h, or 4.7 fish/$m^3 \times 10^6$ of water filtered through the net.

Distribution of Spring Chinook Salmon Smolts

Yearling-sized chinook salmon occurred throughout the spring in 1984. Most fish originated from the estimated 4 million spring chinook salmon released from upper Columbia River hatcheries in late April.

Catches of yearling chinook salmon were greatest at the midchannel station (73%, n =

TABLE 3.—Estimates of proportional distribution (%) for wild versus hatchery populations of 0-Age fall chinook salmon. Shoreline stations were fished only at ~1 m depth.

Month of capture	Net position	Sample station: Shoreline 1	Barge nets 1	Barge nets 2	Barge nets 3	Barge nets 4	Shoreline 2
April/May	Surface	6.7	3.2	2.1	4.8	14.3	4.5
(n = 3,451)	Middepth	—	7.1	2.0	2.8	9.1	—
	Bottom	—	6.9	2.2	3.2	20.9	—
June	Surface	1.4	1.3	5.7	11.3	6.6	0.8
(n = 2,824)	Middepth	—	2.9	2.9	2.8	5.1	—
	Bottom	—	6.9	8.8	21.9	21.6	—

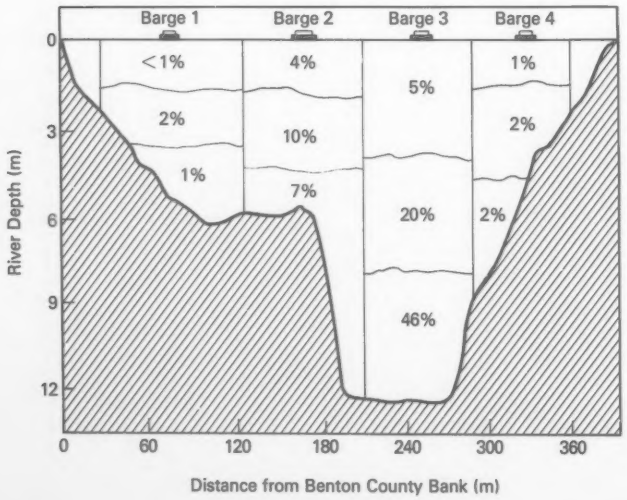

FIGURE 7.—Cross-sectional distribution of yearling chinook salmon (n = 459) caught in shoreline and barge fyke nets during spring 1984. Note: horizontal scale is reduced.

459) (Fig. 7). Catches were low at barges 1 and 4, and no yearling chinook salmon smolts were captured in the shoreline fyke nets. Overall catches were significantly higher ($P \leq 0.01$) from the bottom and middepths at barge 3 than for any other station/depth combination.

The number of spring chinook salmon smolts collected per 100 hours of sampling averaged from 0.3 fish at surface depth (barge 1) to 57.8 fish at bottom depth (barge 3) (Table 4). Although station differences were not as pronounced when CPUE was expressed by volume, the greatest numbers of fish appeared to pass barge 3 in the main river channel.

Spring chinook salmon smolts ranged from 101 to 224 mm FL. Mean size varied little, possibly because most of the fish originated from hatcheries. Scale analysis confirmed that most of the fish (171 of 173) were yearlings.

TABLE 4.—Summary of average catch per unit effort for chinook salmon smolts caught by fyke nets in spring 1984. No smolts No smolts were caught in the shoreline fyke nets.

Station	Depth	Number/h × 10^2	Number/m^3 × 10^6
Barge 1	Surface	0.3	0.4
	Middepth	2.8	3.7
	Bottom	1.8	2.8
Barge 2	Surface	4.2	3.5
	Middepth	10.4	9.5
	Bottom	7.5	7.8
Barge 3	Surface	6.7	4.5
	Middepth	27.3	18.0
	Bottom	57.8	42.6
Barge 4	Surface	1.3	1.7
	Middepth	2.5	3.6
	Bottom	2.1	5.0

Distribution of Sockeye Salmon Smolts

Juvenile sockeye salmon were the third most abundant salmonid group collected at the site. These fish originated from wild stocks in upper Columbia River tributaries, primarily the Okanogan and Wenatchee River systems (Allen 1977). Peak catches of juvenile sockeye salmon occurred in mid–May 1984.

A total of 173 sockeye salmon smolts was collected at the barge stations, but none were captured by shoreline fyke nets. Most of the sockeye salmon smolts (90%) were caught in midstream areas (barges 2 and 3) from the middepth and bottom sets (Fig. 8). Catch profiles indicated that sockeye salmon smolts migrated at greater depths than other salmonids in 1984. Catches from the bottom depth at barge 3 were significantly greater ($P \leq 0.01$) than catches from any other station/depth combination.

Catch per unit effort for juvenile sockeye salmon averaged from 0.3 to 29.2 fish/100 h of sampling, depending on station and depth (Table

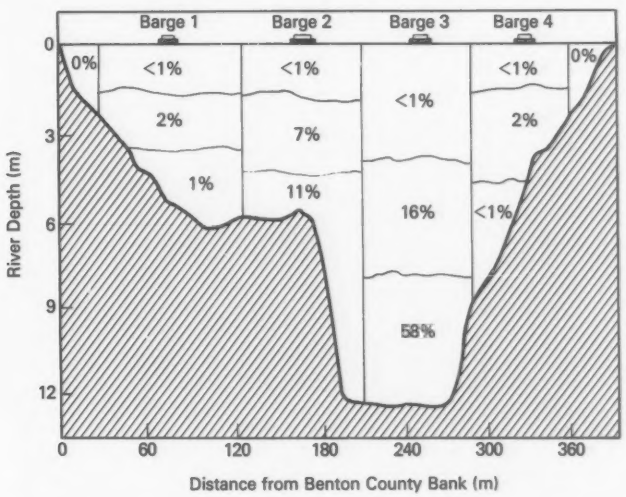

FIGURE 8.—Cross-sectional distribution of sockeye salmon smolts (n = 173) caught in shoreline and barge fyke nets during spring 1984. Note: horizontal scale is reduced.

5). Estimated densities ranged from about 0.2 to 21.6 fish/$m^3 \times 10^6$ of water sampled. Lowest catches were noted for surface sets.

Sockeye salmon were intermediate in size between 0–age fall chinook salmon and spring chinook salmon smolts. Outmigrant sockeye salmon ranged from 74 to 101 mm FL. About 80% of the sockeye salmon were >95 mm FL and, of 96 fish examined, almost all their scales had not yet formed an annulus. Circuli counts for all fish ranged from 8 to 17 and were positively correlated ($R^2 = 0.71$) with fish length.

TABLE 5.—Summary of average catch per unit effort for sockeye salmon smolts caught by fyke nets in spring 1984. No smolts were caught in the shoreline fyke nets.

Station	Depth	Number/h × 10^2	Number/m^3 × 10^6
Barge 1	Surface	0.28	0.35
	Middepth	0.84	1.11
	Bottom	0.59	0.92
Barge 2	Surface	0.26	0.22
	Middepth	2.93	2.67
	Bottom	5.25	5.20
Barge 3	Surface	0.28	0.19
	Middepth	7.25	4.77
	Bottom	29.20	21.64
Barge 4	Surface	0.50	0.67
	Middepth	1.00	1.42
	Bottom	0.26	0.62

Distribution of Steelhead Smolts

Small numbers of juvenile steelhead were collected from late April through early June 1984. Most fish had eroded fins characteristic of hatchery stocks. Various agencies released approximately 1.1 million steelhead smolts into the Columbia River above Priest Rapids Dam in 1984. Almost all juvenile steelhead (34 of 39) were collected in the main river channel (barge 3) and from either the middepth or bottom positions. No steelhead were collected in shoreline fyke nets and only one was collected at a nearshore barge station (barge 4).

An average of 0.3 to 5.4 steelhead were collected/100 h of sampling, depending on the net location (Table 6). Catches were highest from the bottom depth at the midchannel station, where about four fish were collected per $m^3 \times 10^6$ of water sampled.

Size of the juvenile steelhead ranged from 165 to 241 mm FL. Scales of 14 fish were examined: 10 fish were yearlings and 4 were age 2.

Other Salmonids

No juvenile coho salmon were captured, even though about 500,000 juveniles were released about 192 km upriver in May 1984 and some were collected by gatewell dipping at Priest Rapids Dam. One juvenile mountain whitefish, *Prosopium williamsoni*, 77 mm FL, was collected in late May 1984.

Distribution Based on Supplementary Sampling

Chinook salmon were the primary salmonid species collected by electroshocking (Table 7). Numbers of chinook salmon smolts peaked in nearshore areas in early May 1984. Wild 0–age chinook salmon dominated catches in late May, and hatchery-released 0–age chinook salmon dominated in late June. Late-summer migrant chinook salmon smolts were also electroshocked in small numbers from late July to early September 1983. Steelhead comprised 7% of the total (n

TABLE 6.—Summary of average catch per unit effort for steelhead smolts collected by barge fyke nets in spring 1984. No smolts were caught in the shoreline fyke nets.

Station	Depth	Number/h × 10^2	Number/m^3 × 10^6
Barge 1	Surface	0	0
	Middepth	0	0
	Bottom	0	0
Barge 2	Surface	0.26	0.21
	Middepth	0.26	0.24
	Bottom	0.55	0.55
Barge 3	Surface	0	0
	Middepth	2.61	1.72
	Bottom	5.37	3.98
Barge 4	Surface	0	0
	Middepth	0	0
	Bottom	0.26	0.62

TABLE 7.—Seasonal totals for juvenile salmonids caught by boat electroshocker in shoreline transects. Each of two 400 m shoreline transects was sampled four times daily.

Date	Total sample days	Species		
		Chinook salmon	Sockeye salmon	Steelhead
August 1983	4	2	0	0
September 1983	3	4	0	0
April 1984	1	3	0	0
May 1984	5	168	0	3
June 1984	4	191	1	1

= 375) yearling-sized salmonids collected by electroshocking during the spring 1984 studies. Only one juvenile sockeye salmon was collected by boat electroshocking.

Overall, 3,982 0–age chinook salmon and 1 juvenile sockeye salmon were collected by beach seining. Almost all of the chinook salmon captured with seines originated from upstream spawning areas near Vernita Bar. Catches peaked on 17 May with 178 fish/seine haul. Numbers declined in June despite the large numbers of hatchery fish present. The size of 0–age chinook salmon collected with seines (Fig. 9) was similar to those collected with fyke nets in April and May. However, fish collected with barge fyke nets in June (see Figure 5) were generally larger than those collected with seines. No juvenile spring chinook salmon or steelhead were collected with beach seines.

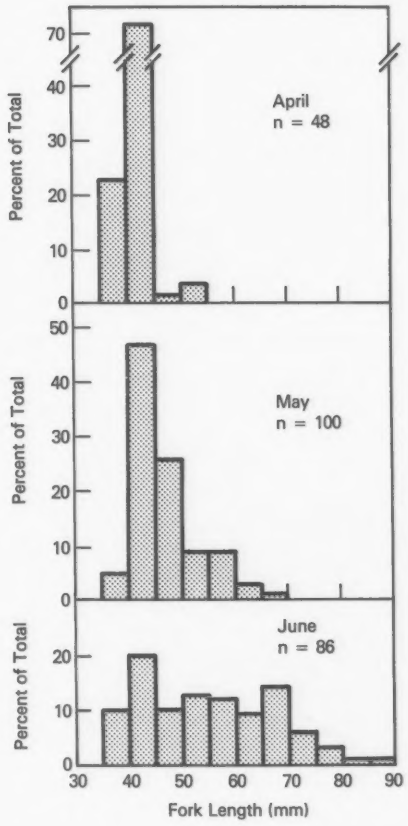

FIGURE 9.—Length-frequency of 0-age fall chinook salmon captured by beach seine in spring 1984.

Diel Patterns In Salmonid Migration

Principal movement of all salmonids occurred between the hours of 2200 and 0400, based on barge fyke net collections; however, differences in peak movement among species were evident from the barge catches (Fig. 10). For example, only 0–age fall chinook salmon (wild and hatchery populations) were collected during daylight hours. For these populations, peak catches occurred just after darkness (2200 to 2400). In contrast, fyke net catches of sockeye salmon, spring chinook salmon, and steelhead smolts peaked between 2400 and 0400. Although nocturnal movement was also evident based on shoreline fyke net catches, a higher proportion (~22%) of the 0–age chinook salmon were collected in shoreline nets during daylight hours (Fig. 11).

Diel patterns of distribution based on electroshock catch totals contrasted among the different groups of chinook salmon (Fig. 12). Peak numbers (55%) of the 0–age fall chinook salmon in April and May were collected from the hours of 1600 to 2200; 44% of the 0–age hatchery fall chinook salmon (June fish) were collected from 0400 to 1000; and 80% of the hatchery spring chinook salmon and late summer migrant chinook salmon were collected during the night from 2200 to 0400.

DISCUSSION

Our studies showed that distributional patterns were different for each of the three most abundant groups of juvenile salmon (i.e., fall chinook, spring chinook, and sockeye salmon). Our hypothesis that fish distribution was independent of barge station and depth was rejected, suggesting that different groups acted differently at different barges and at different depths. Salmonid outmigrants in the Hanford Reach exhibited patterns of proportional distribution that were mainly size related (Table 8). Larger outmigrants (i.e., chinook salmon, sockeye salmon, and steelhead) occurred near the bottom, midchannel zone of the river, while the smaller wild and hatchery 0–age fall chinook salmon preferred the shallower shoreline areas.

The relatively high contribution of fall chinook salmon to the total catch during the spring resulted primarily from the large numbers of wild fish emerging in the Hanford Reach and the hatchery fish released there. About 90% of the salmonids collected were 0–age chinook salmon. Collectively, this group comprised about 70% of

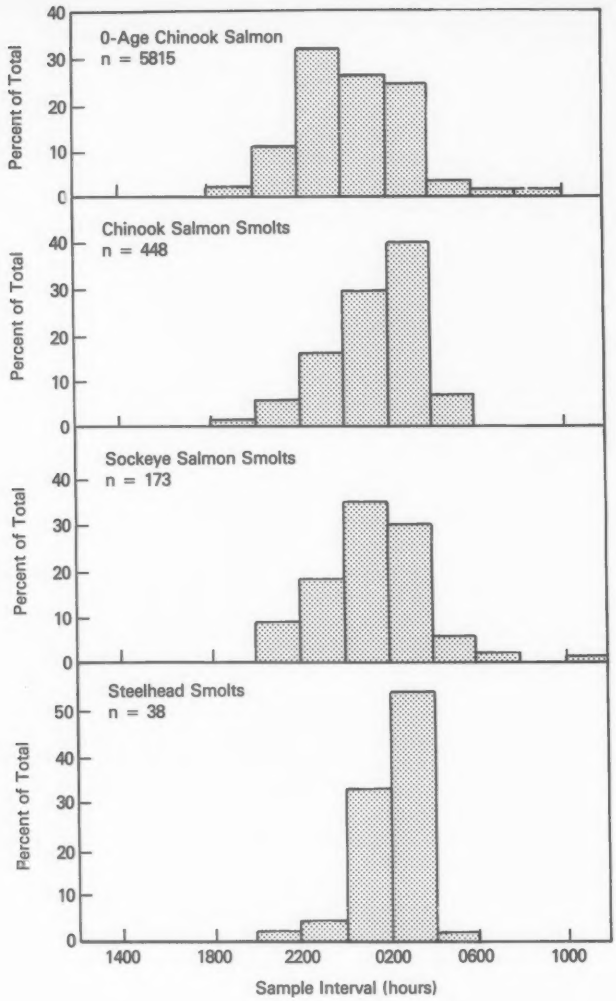

FIGURE 10.—Diel catch patterns of juvenile salmonids collected by barge fyke nets during spring 1984.

the juvenile salmonids estimated to pass the study site in 1984. Wild populations of 0–age fall chinook salmon were more vulnerable to active and passive netting techniques because they were smaller relative to juvenile salmonids produced or released upriver. Because the smaller 0–age fall chinook salmon that emerge from redds at Vernita Bar use the Hanford Reach primarily for temporary feeding and rearing (Becker 1973), their distribution may differ from the distribution of smolts migrating from upstream sites.

The cross-sectional distribution of chinook salmon fry (36 to 70 mm FL) in our collections was similar to that observed by Mains and Smith (1964) for 0–age fall chinook salmon in the Columbia River at river km 550. Although Mains and Smith also reported data from "yearling" outmigrants in June and July, the length (85 to 90 mm FL) of these fish approximated that of later-migrating stocks of 0–age fish from upriver. The spatial distribution described by Mains and Smith for yearlings (based on volume sampled) was nearly identical to the distributions that we obtained for naturally produced stocks of 0–age fall chinook salmon. In both

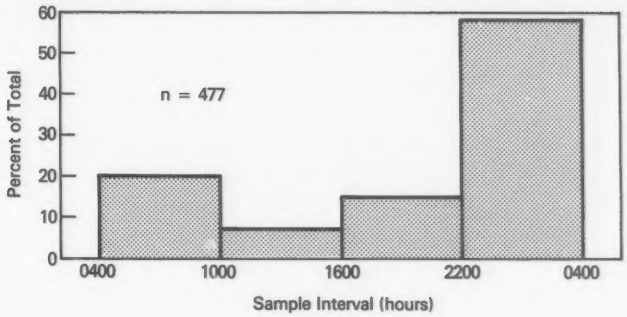

FIGURE 11.—Diel catch patterns of 0-age fall chinook salmon collected by shoreline fyke nets during spring 1984.

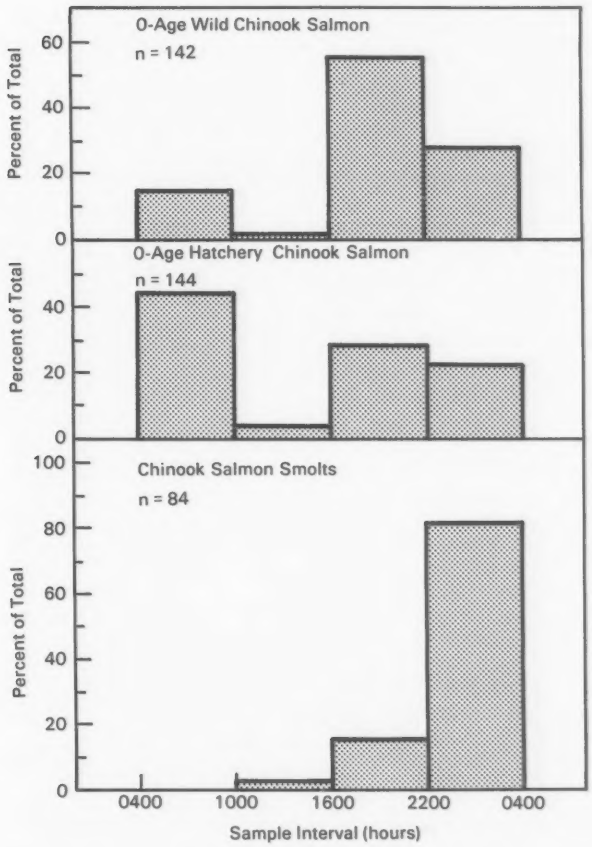

FIGURE 12.—Diel catch patterns of juvenile chinook salmon collected by shoreline electroshocking during spring 1984.

TABLE 8.—Relationship of juvenile salmonid size to fyke net capture location. Key: S1,S2= shoreline stations, B1-B4 = barge stations, s = surface, m = middepth, b = bottom, ns = not sampled.

Population	Mean size (mm)	Depth zone	Proportional distribution (%) S1	B1	B2	B3	B4	S2
Chinook salmon								
0-age fall (wild)	45	s	7	3	2	5	14	3
(*n* = 3,451)		m	ns	7	2	3	19	ns
		b	ns	7	2	2	21	ns
0-age fall (hatchery)	85	s	1	1	6	4	7	1
(*n* = 2,824)		m	ns	3	3	3	5	ns
		b	ns	7	9	22	22	ns
0-age summer migrant	114	s	ns	0	0	9	0	ns
(*n* = 26)		m	ns	0	0	14	5	ns
		b	ns	0	0	73	0	ns
1-age spring	140	s	0	1	4	5	1	0
(*n* = 459)		m	ns	2	10	20	2	ns
		b	ns	1	7	40	2	ns
Sockeye salmon	90	s	0	1	4	5	1	0
(*n* = 173)		m	ns	2	6	16	2	ns
		b	ns	1	11	58	1	ns
Steelhead	200	s	0	0	3	0	0	0
(*n* = 39)		m	ns	0	3	23	0	ns
		b	ns	0	8	62	3	ns

studies, most fish were collected in shoreline areas, but catches from one shoreline were about three times greater than catches from the opposite shoreline. Thus, the physical features of some shorelines appear to influence the distribution of juvenile fall chinook salmon.

Low catches of chinook salmon smolts during the late summer may reflect the small population size in upriver areas. The number of summer and fall chinook salmon spawning above Priest Rapids Dam in 1982 was lower than the 1972–82 10 yr average.[2] The total outmigration of up-river 0–age chinook salmon in 1983 was about 1 million fish (estimate based on escapement of adult summer and fall chinook salmon over Priest Rapids Dam in 1982 and historical production factors), or only 40% of the numbers estimated by Sims and Miller (1977) for the 1976 outmigration. Because the mouth openings of the four barge fyke nets collectively only sample 0.1–0.2% of the river cross section, small sample numbers would be predicted for fish present at low densities.

Species-specific differences in behavior also affected spatial distribution. For example, almost all sockeye salmon smolts were collected from midstream portions of the river. This phenomenon was not entirely consistent with the size-related model of fish distribution noted for the different groups of juvenile chinook salmon. Other studies of lateral distribution have shown that yearling sockeye salmon migrate primarily in midriver, utilizing areas of highest current velocity (Dames and Moore 1982). The apparent preference of juvenile sockeye salmon for the river bottom near our study site also contrasts to that observed for lentic populations, which reportedly migrate primarily near the surface (Johnson and Groot 1963).

Electroshocking and beach seining showed that the shoreline fyke nets could not be used to effectively collect larger juvenile salmonids. Although differences in gear effectiveness make direct comparison of methods impossible (Hulbert 1983), it appears that nearshore estimates of distribution based on shoreline fyke net catches were low. For example, spring salmon and steelhead smolts were sometimes electroshocked at night in nearshore areas ~1 m deep, but none were collected in shoreline fyke nets that were fished at similar depths. Daytime catches in shoreline fyke nets were also low when compared with the observed densities of

[2]Rod Woodin, Washington Department of Fisheries, Olympia, WA 98504, pers. commun. November 1983.

0–age chinook salmon during seining. For some species, active sampling techniques helped support distribution trends observed from fyke net data. For example, the preference of migrating sockeye smolts for offshore areas was also indicated by the absence of sockeye salmon in nearshore collections using electroshocking and seines.

In our study, hatchery-reared 0–age chinook salmon (range 75 to 90 mm FL) were less abundant in shallow nearshore areas than wild stocks. This spatial segregation was evident for both seining and fyke net collections. Thus, differences in distribution patterns that may be attributed to size, season, or physiological condition were also evident.

Diel movement patterns were consistent with those observed in previous studies of migrating juvenile salmonids in the Columbia River. Principal movement of outmigrating juvenile chinook salmon occurred during the night at Priest Rapids Dam (Sims and Miller 1977) and at Byers Landing (Mains and Smith 1964). Smith (1974) collected 91% of primarily 1-age juvenile chinook salmon at night in impounded waters on the Snake River. Sockeye salmon have also shown a preference for nocturnal movement in other river systems (Kerns 1961; Dames and Moore 1982). In general, natural light intensity appears to be the major environmental factor controlling diel migration patterns of salmonid fry (Godin 1982).

The observed patterns of diel behavior may have affected the cross-sectional distribution of the juvenile salmonids. For example, we observed that spring chinook salmon smolts were often abundant just after sunset in shallow nearshore areas (≤30 cm deep) of low current velocity. This inshore appearance may have preceded active or passive downstream movement. Nighttime movement into the current may result from a loss of visual contact with the surroundings (McDonald 1960) or a reduction of rheotactic response (Hoar 1953). Both of these mechanisms could result in passive downstream displacement; however, there were distinct differences in diel timing among the four species collected. These differences suggest that migration is not controlled solely by passive mechanisms.

Documented migration rates of juvenile salmonids in the Columbia River are consistent with activity rhythms that include feeding, quiescent behavior, and active migration. At midstream velocities averaging 1 m/s, a passively drifting fish would travel about 29 km in an 8 h night. Migration rates would be faster with higher current velocities, as occurs during the spring freshet (2–3 m/s), or for actively migrating fish. Most salmonid smolts apparently migrate actively in midchannel for only a few hours daily since reported mean migration rates of juvenile salmon through the Hanford Reach are about 56 km/d (Weitkamp and McEntee 1982). The patterns of distribution that we observed probably provide only a partial description of the interacting behavioral characteristics that increase species survival and efficient use of energy reserves.

ACKNOWLEDGMENTS

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Time Series of Growth in the Genus *Sebastes* from the Northeast Pacific Ocean

George W. Boehlert, Mary M. Yoklavich, and Dudley B. Chelton

ABSTRACT: Marine fish populations respond to their physical and biotic environment in complex ways. While direct studies may discern short-term responses at the individual level, time series are needed to describe or predict the population level response to environmental variation or cycles. The ageing technique presented in this paper extracts historical growth information from otoliths through sectioning and careful measurement in order to establish time series of growth. Otoliths of two long-lived species, *Sebastes pinniger* and *S. diploproa*, were collected off the west coast of North America in 1977–84. Fish ages ranged from 1 to 86 years; corresponding birth dates were as early as 1896. Otolith measurements allow description of growth at ages 1–6 for several decades of this century. Although the technique has certain limitations, significant interannual variability in growth is observed, and its relationship to the species' environment is interpreted. Within species, coherence in growth among age groups was not always evident; first year growth in *S. diploproa* was particularly different from growth in other years. For both species, growth responses to environmental factors were not clear; the dominant signal in the time series appears to be increased growth rates after about 1970. This signal is apparently related to density-dependent factors (most likely prey availability) associated with stocks depleted by fishing pressure.

Long-term changes in marine fish populations can be caused by physical and biotic factors as well as man-induced changes. An important goal of fisheries research is to evaluate the effect of fishing on population levels, and this task is easily accomplished if natural variability is understood. Determining causal relationships and superimposing fishing mortality can lead to predictive capability; indeed, many studies in fisheries oceanography model past changes in fish stocks with the objective of forecasting future trends in populations for purposes of fisheries management. Long-term biological data sets are also valuable for ecosystem research, particularly in evaluating the range of natural variability (Wolfe et al. 1987). Historical catch records have been used to assess long-term changes in marine fish populations or stock sizes, and such data from many decades are available for some Pacific salmonid stocks (Mysak et al. 1982; Rogers 1984), for several North Atlantic fisheries (Cushing 1982), and in the Southern Hemisphere for Tasmanian fish populations (Harris et al. 1988). Changes in species assemblages and biotic interactions in the California Current region have been described on both the decade scale (Loeb et al. 1983; Moser et al. 1987) and the century scale (Soutar and Isaacs 1974).

Long-term time series are developed either from continuous data collection or by the extraction of information stored naturally as a chronographic record. Continuous data collection must occur over generations of biologists; starting a new series may not allow achievement of objectives for 30 or more years, so available time series, which are often collected for other purposes, are used. A classic example of extracting data from a chronographic record is the study of fluctuations in population abundance of *Engraulis mordax*, *Sardinops sagax*, and *Merluccius productus* by Soutar and Isaacs (1974). By enumerating fish scales preserved at different depths in anoxic, varved sediments, they defined natural cycles of abundance of these species over 150 years. This approach has recently been applied by Shackleton (1987). Chronological information is also stored in fish otoliths (Radtke 1984; Campana and Neilson 1985). Estimating age of fishes and using otoliths for back calculation are simple examples of extraction of historical information. In addition, the isotopic composition of otoliths has been used to define past thermal habitats occupied by individual fish (Mulcahy et al. 1979; Radtke 1987) and to identify stocks (Mulligan et al. 1987).

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Because studies on fish growth are generally conducted at a single time, time series on the order of several decades are either rare or absent. Some available time series are often produced from different studies, which may not have used the same techniques for sampling, ageing, or interpretation (Boehlert and Kappenman 1980). Using fish scales and interopercular bones from two flatfish species collected over approximately 15 years, Kreuz et al. (1982) established time series of growth and found that growth was negatively correlated with temperature. Width and length of otoliths can be used to estimate length of fish so that past growth patterns can be estimated with back-calculation techniques on otoliths from older fish. Extreme longevity has been documented in the scorpaenid genus *Sebastes* (Bennett et al. 1982; Leaman and Nagtegaal 1987), and ages in excess of 80 years have been reported for several species (Archibald et al. 1981; Boehlert and Yoklavich 1984; Leaman and Beamish 1984). Thus, otoliths of these species can potentially be used to estimate growth from several decades ago.

In this paper, we describe an otolith-based technique for obtaining a historical time series of growth. We apply this technique to two species, the canary rockfish, *Sebastes pinniger*, and the splitnose rockfish, *S. diploproa*, and describe the resultant time series of growth in light of physical and biological factors.

MATERIALS AND METHODS

Otoliths from *S. pinniger* and *S. diploproa* were collected during rockfish surveys conducted by the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, in 1977 (Boehlert 1980), 1980 (Boehlert and Yoklavich 1984), and 1983 (Wilson 1985). Collection techniques followed Gunderson and Sample (1980). Our objective was to represent as many years of growth as possible; therefore, otolith selection was based upon age alone, and old fish greatly outweighed their relative abundance in a random sample. Additional otoliths from *S. pinniger*, collected off the central Oregon coast in 1984, were obtained from the Oregon Department of Fisheries and Wildlife.

Technical aspects of our methods, described in Boehlert and Yoklavich (1987), are repeated here for completeness because the original information is not widely available. For otolith sectioning and age determination, we followed Boehlert and Yoklavich (1984). Briefly, otoliths were affixed to cardboard tags, embedded in polyester casting resin, mounted on a diamond lapidary saw, and fed onto a pair of thin diamond blades separated by acetate spacers. Dorsal-ventral sections through the focus and perpendicular to the sulcus, approximately 0.4 mm thick, were removed from the center of the otolith, attached to microscope slides, and ground to eliminate artifacts. Total ages were determined from these sections by identifying the first translucent annulus (winter growth zone) and counting sequential growth zones from the center toward the dorsal edge; dorsal annuli at ages near 8–10 years were followed from the dorsal edge to the interior dorsal quadrant, and subsequent annuli were counted to the internal surface.

Annulus measurements, used as a proxy of annual fish growth, were limited to the first 6 years of growth. This limit was imposed because otolith increments became smaller with increasing age; eventually, linear growth stopped, and the otolith began to thicken (Bennett et al. 1982; Boehlert 1985). Two different techniques for otolith measurement were used. In the faster growing *S. pinniger*, whose otoliths are clearer, measurements were from the focus to the dorsal distal edge of each increment (Fig. 1). In *S. diploproa*, whose otoliths are typically more opaque and whose annual increments are smaller, the focus was difficult to identify; for this species, measurements were from the dorsal to ventral distal edges of increments 1–6.

Data from each fish included sex, fork length, date of collection, location, total age, and widths of the increments measured from the otoliths for ages 1–6. The first increment width was a true reflection of first year growth; subsequent measurements, however, integrated past growth. That is, a large growth increment in year 1 could bias the measurement in years 2–6. To remove this correlation and to provide a measure of growth in each year, our analysis used growth increments (GI(i), where i = 1–6) determined by differencing successive measurements. Thus, growth in a given year was not cumulative and generally did not reflect past growth.

Age was subtracted from the year of collection to determine the year of birth. For each fish, each growth increment (1–6) was associated with a specific "year of growth" in the following manner: Increment 1 represented the year of birth or first year growth, increment 2 represented the following year, and so forth. Data on 6 years of growth were available for each fish with the ex-

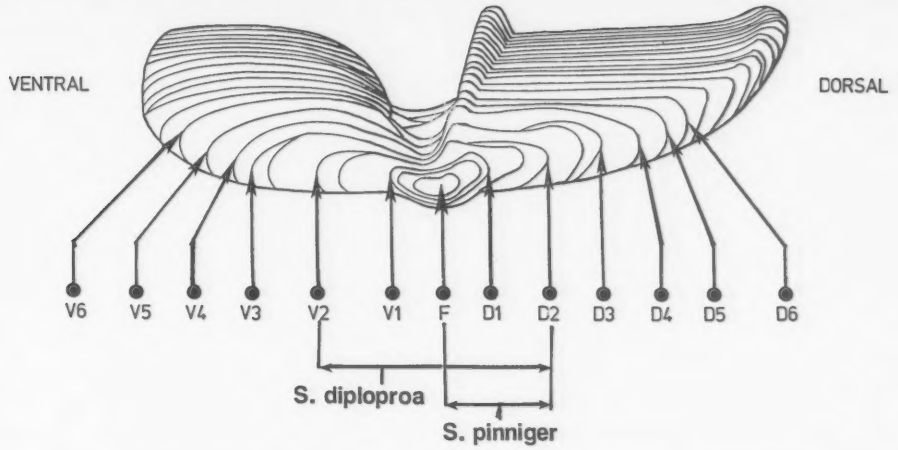

FIGURE 1.—Schematic drawing of an otolith section from *Sebastes* spp. showing the axes of measurements. Measurements for *S. pinniger* were from focus to dorsal distal increment margin (i.e., F to D2); measurements for *S. diploproa* were from dorsal to ventral distal increment margins (i.e., V2 to D2).

ception of those younger than 6 at the time of sampling. As an example, a fish collected in 1980 and aged at 40 years was determined to be born in 1940; therefore, growth measurements from this individual were available for years 1940 (GI(1)) through 1945 (GI(6)).

Most otoliths in our study were from males; otoliths from older females were also included to increase the sample size earlier in the time series. Length at age for these species did not differ between sexes until after sexual maturity, which occurred after age 6 (Boehlert 1980; Boehlert and Kappenman 1980). Still, to test for differences in growth between sexes, we separated the data by sex and then aggregated the data for each GI(i) so that each year of birth had a single, mean value. A paired t-test was used to test for differences in respective growth increments for all years in which both male and female data were available. Growth did not significantly differ between sexes for either species ($P > 0.10$), so data were combined in subsequent analyses.

Certain aspects of the technique, associated with errors in otolith increment measurement and age estimation, may have led to variability in results. From a methodological standpoint, three errors were quickly apparent. First, small changes in the location where the section was removed from the otolith (Fig. 1) may have resulted in slightly different increment measurements; we expected this to introduce relatively minor errors, however, since the sectioning technique (Boehlert and Yoklavich 1984) was designed to be the same. The second source of error occurred in the estimate of total age. Errors in this estimate will result in the assignment of an incorrect year of birth and, thereby, incorrect years of growth for each growth increment; this type of error is probably the most serious, because it will tend to decrease the reliability of real differences between adjacent years. This type of error will increase with increasing age (Boehlert and Yoklavich 1984), and therefore, the reliability of between-year differences in growth will decrease somewhat with increasing age. Finally, errors in selection of annuli (for example, selecting 2–7 instead of 1–6) can occur when making measurements on the section. The cumulative effects of these errors, averaged over many individual samples for each year, should not significantly mask long-term trends in the data. The errors could mask correlations with high frequency environmental features but should not affect correlations with low frequency phenomena.

An additional concern stemmed from the implicit assumption that there is no linkage between longevity and growth; this concept, associated with Lee's phenomenon, is related to size-selective mortality (Ricker 1969). If long-lived individuals are characterized by either faster or slower growth rates during the first 6 years of life than are individuals with shorter lifespans, then we can encounter problems comparing growth of young and old fishes. In lightly

exploited populations of *S. alutus*, for example, very old age groups may have smaller mean lengths than younger age groups, suggesting some type of growth-dependent mortality (Leaman[1]). Markedly smaller mean lengths at age have not been observed, however, for very old specimens of either *S. pinniger* or *S. diploproa* (Boehlert and Yoklavich 1984; Wilson 1985). A genetic basis for differences in growth and age at sexual maturity has been suggested for cod, *Gadus morhua* (Borisov 1979) and brown trout, *Salmo trutta* (Favro et al. 1979). An investigation of the biochemical genetics of *S. diploproa* by using electrophoresis at 29 loci has shown no variation associated with age (L. W. Seeb and G. W. Boehlert unpubl. data). Although negative results cannot rule out a difference, our growth results did not show a consistent trend supporting a genetic basis for growth differences.

Data Analysis and Interpretation

Yearly means of GI(i)'s were calculated and were the values upon which further analysis was made. Standardized growth anomalies (Z-scores) were calculated so that each time series of growth for both species had a mean of zero and a standard deviation of one. This allowed comparison of the growth anomalies in different growth years, standardized for the effects of growth increment magnitude. Comparisons between species were also facilitated by this conversion. A growth anomaly value of zero corresponded to normal growth rate, averaged over the period of the data record.

Within species, there were both similarities and differences between the time series of different age groups. Covariability between different age groups was extracted by principal component analysis (Hotelling 1933) of the six-by-six cross correlation matrix, which expressed interrelationships among the six series of standardized growth anomalies of each species over the period of analysis. The principal component expansion of growth increments can be written as

$$\mathrm{GI}(x,t) = \sum_{n=1}^{6} F_n(x) a_n(t); \qquad (1)$$

where x is the age class (1–6), t is time, and the index n corresponds to component number (1–6). The loadings $F_n(x)$ are the eigenvectors of the cross correlation matrix. The amplitude time series $a_n(t)$ are referred to as the principal components of covariability. The dominant loadings across age groups (those reducing the largest proportions of total variance in the original data set) and the associated principal component time series were interpreted in terms of physical and biological processes influencing growth rate variability. An attempt was made to relate the principal component time series as dimensionless, uncorrelated expressions of growth for each species to time series of environmental and biological data. Environmental data (upwelling, wind speed, and wind stress curl at lat. 45°N, long. 125°W; sea-surface temperature at Neah Bay, WA, lat. 48°22′N) from 1946 to 1977 were provided by the Pacific Fisheries Environmental Group, Monterey, CA. Sea level data from San Francisco (lat. 38°N) were taken from Prager and MacCall[2].

RESULTS

A total of 942 *S. pinniger* (616 males and 326 females) and 802 *S. diploproa* (651 males and 151 females) were used in this study. Specimens of *S. pinniger* ages 2–60 years corresponded with birth dates from 1920 to 1978 (Fig. 2A); *S. diploproa* ages 1–86 years corresponded with birth dates from 1896 to 1979 (Fig. 2B). Total numbers of growth increments measured were 5,600 for *S. pinniger* and 4,714 for *S. diploproa*.

Mean annual size of growth increments for both species showed a reduction with age group, which is typical in fishes. Mean size of increments decreased dramatically (between twofold and threefold) from age groups 1 and 2, then slowly from age groups 2–6 (less than twofold). Growth anomalies for all ages were characterized by significant interannual variability for both species (Figs. 3, 4). The standardized time series for *S. pinniger* (Fig. 3) showed a general, gradual decreasing trend in growth rates for age groups 2–4 from the beginning of the record until about 1965 or 1970. Age group 1 showed a generally decreasing trend prior to about 1957 and an increasing trend thereafter. Age groups 5 and 6 showed a gradually increasing trend virtually

[1]B. M. Leaman, Pacific Biological Station, Nanaimo, B.C., Canada, pers. commun. November 1987.

[2]Prager, M. H., and A. D. MacCall. 1986. An environmental data base describing coastal southern California in the years 1920–1984. Part I: Procedures and summaries. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Adm. Rep. LJ-86-31, 50 p.

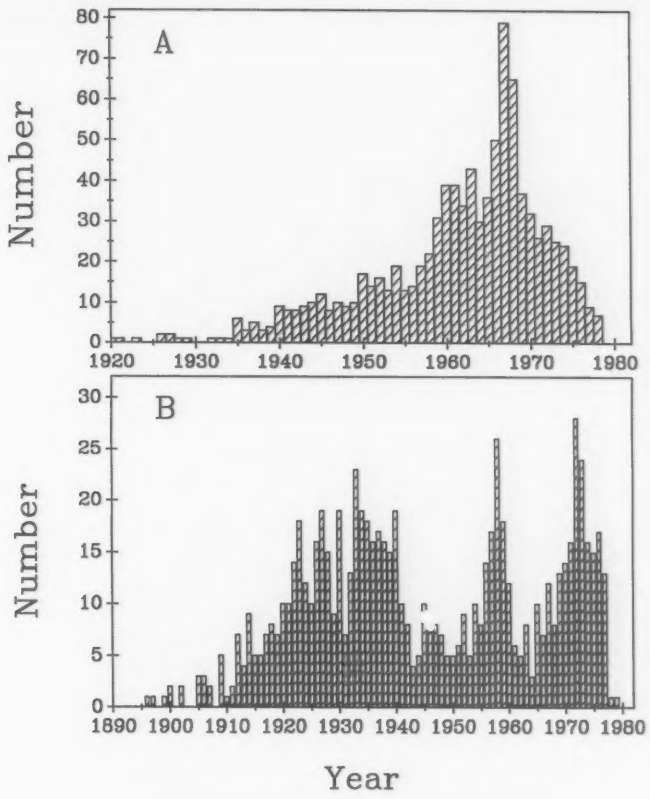

FIGURE 2.—Distribution of the years of birth; males and females are combined. A. *Sebastes pinniger*. B. *S. diploproa*.

throughout the time series. After about 1972, all age groups showed concordance in a relatively abrupt increase in growth rates. This increase may have been shorter lived for age groups 5 and 6, as suggested by the decrease in positive growth rates for the last few years of the record. Positive growth rates continued to increase to the end of the record in the 5 yr running averages for age groups 1–4, though with some significant year-to-year variability in the yearly data.

The time series for *S. diploproa* (Fig. 4) was much longer than for *S. pinniger* (Fig. 3). Age groups 2–4 generally showed a gradual decreasing trend in growth rates prior to about 1965 or 1970. This pattern was similar to that observed for *S. pinniger* age groups 2–4 over the more limited record length. This long-term trend in decreasing growth rates was less evident in *S. diploproa* age groups 1, 5, and 6. Growth rates for age group 5 were nearly normal throughout the record. Growth rates for age group 6 were relatively low in the early part of the record and slightly higher than normal for the period 1930–55. They decreased briefly from 1955 to 1960, then were steady, near-average, or slightly increasing until about 1970. Age groups 2–6 of *S. diploproa* increased in growth rates during the 1970's, coinciding with the high growth rates of all age groups of *S. pinniger* after about 1972. Growth rates for age group 1 of *S. diploproa* were strikingly different from all other age groups of both species of *Sebastes*, with a predominance of variability over much shorter time scales (ca. 5 years) and no evidence of a rapid increase during the 1970's.

The relationship between growth variability in different age groups summarized above from the time series in Figures 3 and 4 were compactly described by the principal components of the six age group time series. We included only years for which yearly mean values of growth were

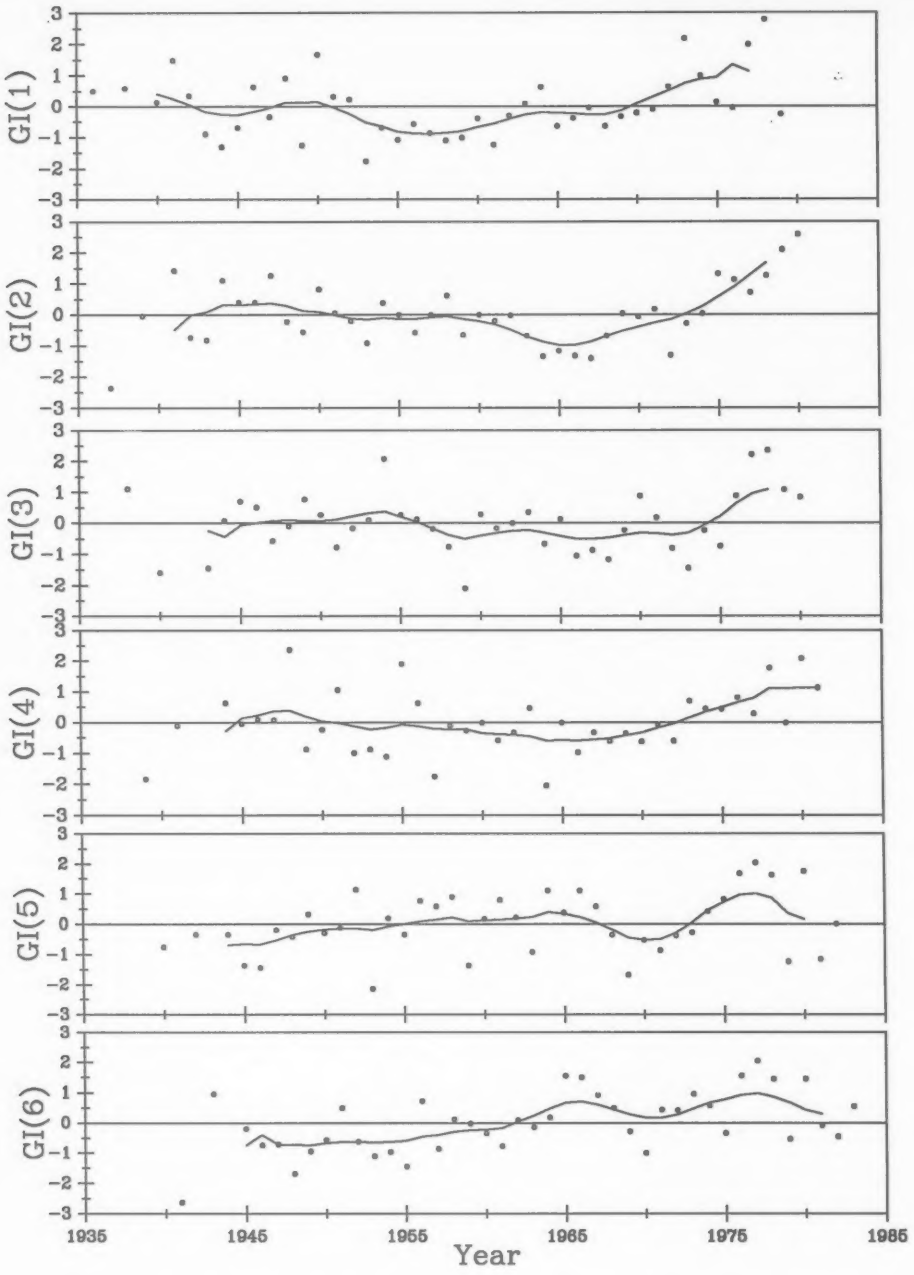

FIGURE 3.—Plot of mean growth anomalies in years of growth 1–6 for *Sebastes pinniger*. Data points represent the yearly mean growth anomalies; the curve represents the double 5-yr running average. Only years with means based upon four or more observations are used.

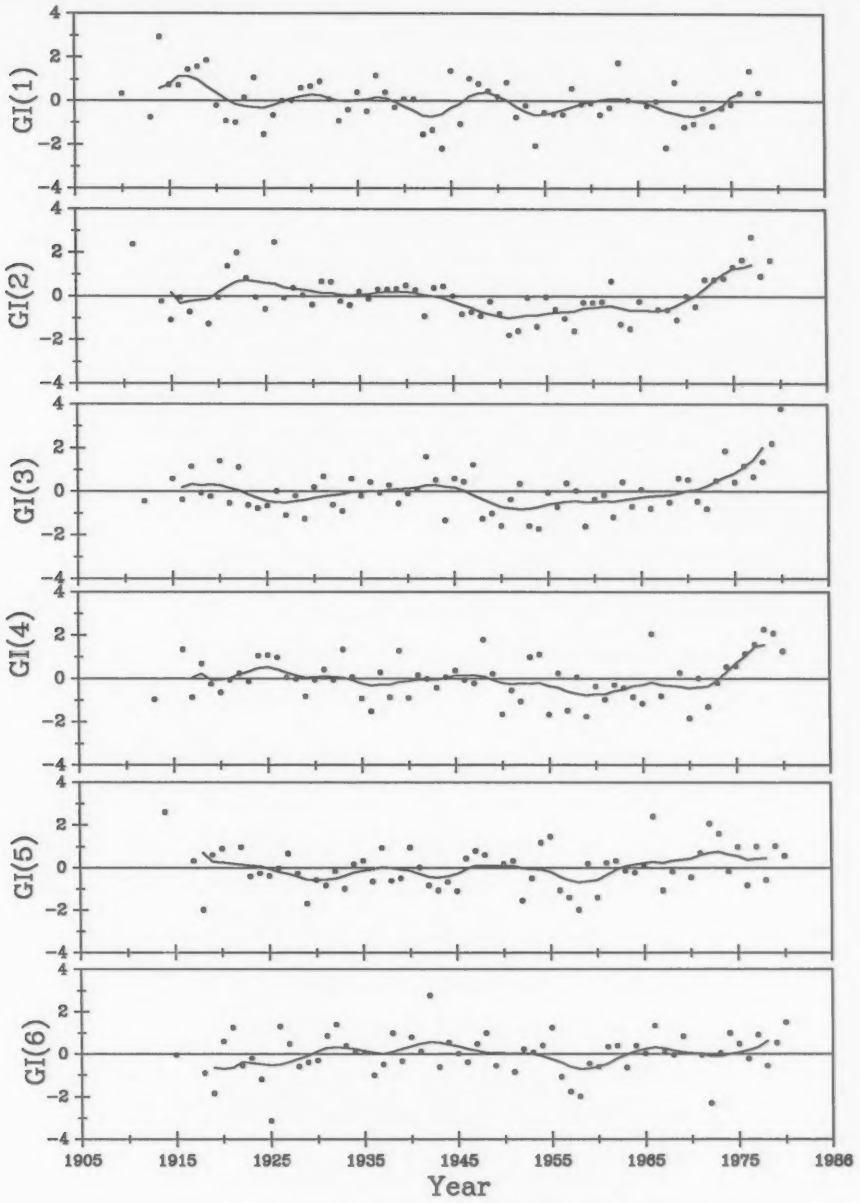

FIGURE 4.—Plot of mean growth anomalies in years of growth 1–6 for *Sebastes diploproa*. Data points represent the yearly mean growth anomalies; the curve represents the double 5-yr running average. Only years with means based upon four or more observations are used.

computed from four or more observations. The first three principal components of *S. pinniger* variability explained 75% of the total variance summed over the six growth anomaly time series; loadings are shown in Figure 5A. Corresponding principal component time series (Fig. 6), or "modes of variability," effectively filter the data to draw attention to the dominant signals discussed above (Fig. 3). By considering the loading values (and thus the relative contribution of each age class) along with the trends in the principal component time series, we described the dominant signals in the time series of the original data. The loadings of the first mode were approximately the same for all six age groups (Fig. 5A); this principal component represented the dominant mode of coherent variability with about the same amplitude in all age groups. The corresponding principal component time series (Fig. 6) is nearly averaged from 1940 to 1970, followed by an abrupt increase beginning about 1972, and represented the high growth rates for all age groups after 1972 (cf. Fig. 3). This was the most pronounced signal in the record, accounting for 36% of the variability over the six age groups.

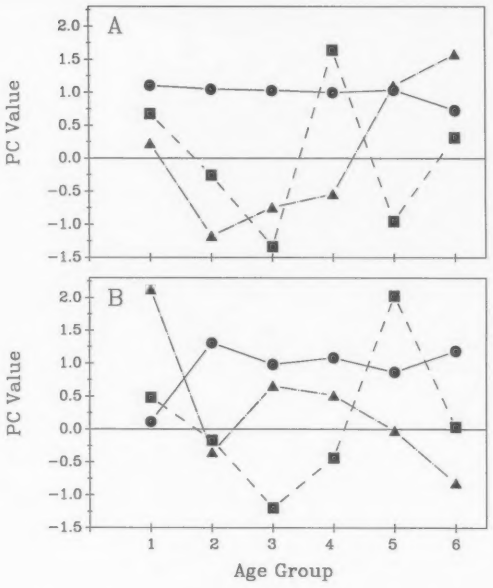

FIGURE 5.—Component (age group) loadings to the three principal components (PC's) explaining the greatest amount of variability in the growth time series. A. *Sebastes pinniger*. B. *S. diploproa*. Circles represent the loadings of the first PC, triangles the second, and squares the third.

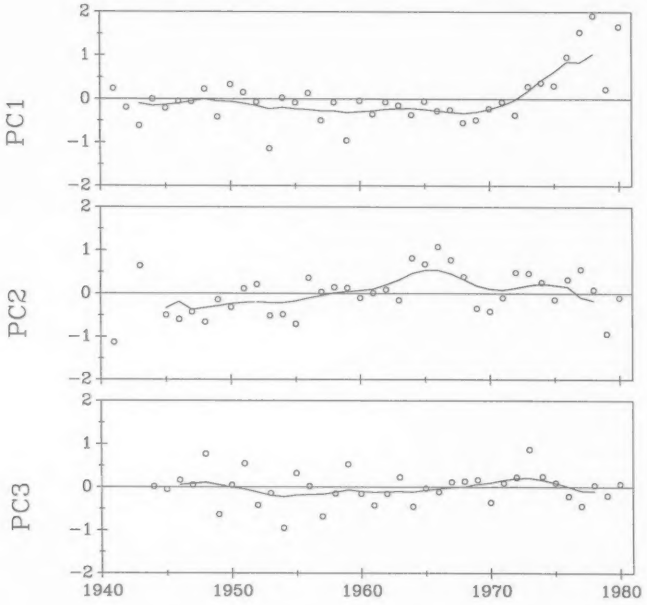

FIGURE 6.—Principal component time series for the three modes explaining 75.0% of the total variance in growth of *Sebastes pinniger* from the six time series in Figure 3. The curve represents the double 5-yr running average.

The second principal component of *S. pinniger* growth variability extracted the coherent trends in the time series evident prior to 1965 (Fig. 3). The loadings (Fig. 5A) were negative for age groups 2–4 and positive for age groups 5 and 6; the loading value for age group 1 was zero, indicating that its variability is not related to this mode. The principal component time series of this second mode of variability (Fig. 6) generally showed a gradually increasing trend from 1945 to 1965, followed by a decreasing trend thereafter. This time variability described well the trends evident in Figure 3 for age groups 5 and 6, for which the loading values (Fig. 5A) were positive. Since the loading values of the second mode were negative for age groups 2–4 (Fig. 5A), this mode of variability (the product of the loading value and the principal component time series, see Equation (1)) corresponded to a gradually decreasing trend in age groups 2–4 growth rates prior to 1965, followed by an increasing trend thereafter. We have no explanation for the difference in the early trends in growth between age groups 5 and 6 and age groups 2–4. Further, growth increments in 1964–68 (Fig. 3) reinforced this difference and produced a peak in the principal component time series in those years (Fig. 6). This second mode of variability describing the trends in growth rates accounts for 24% of the variance in the data.

The loading values of the third principal component of *S. pinniger* growth variability (Fig. 5A) showed no obvious coherent relationship among age groups. The values oscillated from positive to negative among the age groups, and the corresponding principal component time series (Fig. 6) showed no remarkable characteristics. Thus, this mode of variability has no obvious physical interpretation.

The first four principal components of *S. diploproa* variability explained 81% of the total variance summed over the six growth anomaly time series; the loadings for the first three modes are shown (Fig. 5B), with corresponding principal component time series (Fig. 7). The loading values of the first principal component, accounting for 30% of the variance, were approximately the same for age groups 2–6 and zero for age group 1. This highlighted the fundamental difference between growth rate variability in age group 1 and that in the other age groups.

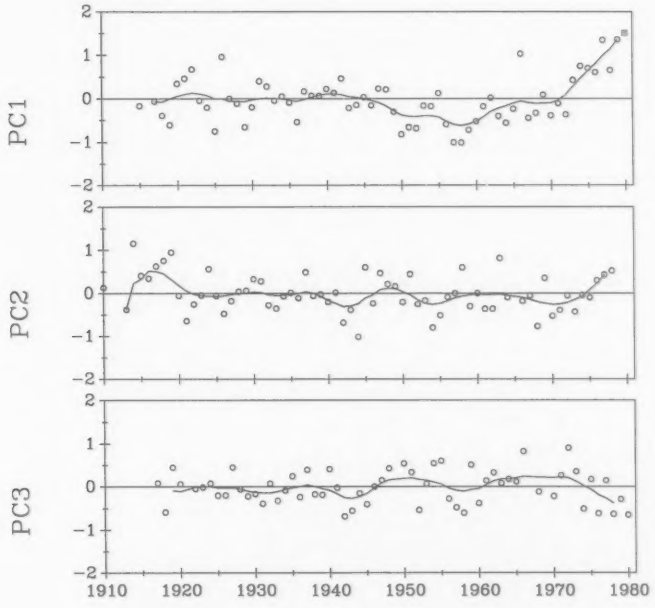

FIGURE 7.—Principal component time series for the three modes explaining 64.6% of the total variance in growth of *Sebastes diploproa* from the six time series in Figure 4. The curve represents the double 5-yr running average.

The principal component time series of this first mode of variability (Fig. 7) showed growth rates as nearly normal in 1915–45, moderately decreasing in 1945–70, and abruptly increasing after about 1972. This was consistent with the earlier interpretation of variability in the individual time series (Fig. 4). The increased growth rates after 1972 coincided with the same signal described by the first principal component of *S. pinniger* growth rates (Fig. 6).

The second principal component of *S. diploproa* growth rates extracted the independent nature of variability in age group 1 and accounted for 19% of the total variance over the six growth anomaly time series. The loading values of this second mode of variability (Fig. 5B) were near zero for all age groups except age group 1. The corresponding principal component time series (Fig. 7) was almost identical to the time series of *S. diploproa* age group 1 (Fig. 4); periods of positive, normal, and negative growth rates in both time series closely corresponded. This further supported the interpretation of this mode of variability as describing age group 1 growth rates. As will be expanded upon in the following section, the lack of linkage between growth rates in age group 1 and the other age groups is likely related to the fact that *S. diploproa* inhabits an environment during the first year of life that is quite different from that during later states of life (Boehlert 1977) and is thus subject to different environmental factors influencing growth rates.

As with *S. pinniger*, the third principal component of *S. diploproa* growth rates has no obvious physical interpretation. The loading values (Fig. 5B) oscillate from positive to negative across the age groups, and the principal component time series (Fig. 7) was nearly normal over the entire record length.

DISCUSSION

The study of growth in marine fishes has typically been concerned with relatively short-term trends in growth of cohorts or populations, most often with fished stocks. Differences in growth may have existed between stocks (Templeman and Squires 1956; Borisov 1979), geographical regions (Boehlert and Kappenman 1980), stock densities, and years (Margetts and Holt 1948; Jones 1983). Such growth differences may be due to genetic factors (Borisov 1979), density dependence (Margetts and Holt 1948; Peterman and Bradford 1987), or environmental factors, most importantly temperature (Brett 1979; Kreuz et al. 1982). The dramatic reduction in stock sizes of many *Sebastes* spp. (Archibald et al. 1983; Ito et al. 1987) has led several authors to suggest density-dependent increases in growth (Gunderson 1977; Boehlert and Kappenman 1980). Recent changes in ageing methodology for *Sebastes* (Boehlert and Yoklavich 1984), however, have rendered long-term comparisons of growth difficult without a historical collection of otoliths.

Analogous to historical time series derived from tree rings (Fritts 1976), the technique described in our paper uses uniform methodology to develop time series of growth for long-lived fishes. Reading of otoliths, however, has more inherent variability than that for tree rings, and the resultant ageing biases described earlier must be considered. The impacts of ageing errors will be most apparent in high frequency signals in the time series and are probably not well resolved by our data; this is the main reason we used the running averages to low-pass filter the data, making the low frequency signals more apparent to the human eye (Figs. 3, 4, 6, 7).

An interesting biological feature of our results is the differing pattern of growth of age group 1 *S. diploproa* (Fig. 4), the only age group not contributing significantly to the variance described by the first principal component for either species. In contrast, first year growth in *S. pinniger* was similar to that in age groups 2–6. *Sebastes pinniger* have a relatively narrow seasonal spawning peak (Westrheim 1975; Gunderson et al. 1980), and pelagic young apparently recruited to their juvenile benthic habitats within about 6 months (Richardson and Laroche 1979). *Sebastes diploproa*, however, seemed to spawn during most months of the year (Snytko 1975), and pelagic prejuveniles were present year-round, at least in the Southern California Bight (Boehlert 1977). Assuming that the first annulus is laid down on a seasonal basis, first year growth was probably quite variable. Further, *S. diploproa* are deepwater (200–500 m) members of this genus, but their first year is spent in surface waters, probably in the upper meter of the water column (Boehlert 1977, 1981); thus, the factors influencing growth in the first year may differ from those affecting growth in subsequent years. Temperature can have an important impact on juvenile rockfish growth (see summary in Boehlert and Yoklavich (1983)), but it may not show coherent cycles be-

tween deep and shallow water over the continental shelf off Oregon (Kruse and Huyer 1983); thus, differences between growth rates for age group 1 and later age groups are not surprising.

The dominant signal apparent in all of the time series of growth, except age group 1 of *S. diploproa* (Figs. 3, 4), and in the first principal component for both species (Figs. 6, 7) was that of increased growth after about 1972. Many of the fish used to calculate the growth anomaly values for this period would have been captured before the age at full recruitment to the fishery, which is 12 years for *S. pinniger* (Wilson 1985) and 14 years for *S. diploproa* (Boehlert 1980). A potential concern with the use of fish younger than the age at full recruitment is that the gear will be selective for larger, faster growing individuals; thus, fish younger than the age at full recruitment might conceivably be characterized by more rapid growth rates, resulting in the increased growth rates observed late in the time series (Figs. 3, 4). If true, then the size of growth increments for fish born in a given year should decrease with time from first recruitment until the age at full recruitment (as is true in Lee's phenomenon). Our samples, however, were taken with sampling gear of much smaller mesh than used in the commercial fishery (Gunderson and Sample 1980). Nonetheless, to test for more rapid growth of younger age fish, we compared the six growth indexes of *S. pinniger* born in 1973–77 and collected in 1980 (N = 41, ages 3–7) with those collected in 1984 (N = 51, ages 7–11). This timespan covered the most rapid increase in growth (Figs. 3, 4). The growth indexes did not significantly differ (paired t-test, $P > 0.10$); this suggests that the size of growth increments did not change as fish born in 1973–77 were collected 4 years closer to the age at full recruitment (1984 versus 1980).

An alternative explanation of increased growth in the 1970's was density dependence. Density-dependent growth has been observed in a variety of fish stocks, generally in association with exploitation (Margetts and Holt 1948) or strong year classes (Jones 1983), and is most evident in immature fish (see summary in Ware (1980)). There is little question that stocks of several *Sebastes* spp. have declined under the influence of fisheries (Gunderson 1984; Bracken 1987; Lenarz 1987; Westrheim 1987). Ito et al. (1987) have suggested that stocks of *S. alutus* off Oregon, Washington, and British Columbia declined from a virgin biomass of about 144,000 metric tons (t) to about 13,500 t in the early 1970's. No direct work documents density-dependent changes in growth in this species, although Gunderson's (1977) model of the stock used increased growth as a compensatory mechanism at low stock density. The best evidence for density-dependent growth changes in the genus is for *S. mentella* (Sorokin et al. 1986). For *S. diploproa*, length frequencies from 1977 (Boehlert 1980) were shifted to much smaller sizes than those from 1961 to 1962 (Alverson et al. 1964); this decrease may have been a result of fishing pressure (Boehlert 1980). Faster growth in the region north of California has been described for this species (Boehlert and Kappenman 1980); density-dependent growth increase (since the major stock reduction occurred in the north) was suggested as one of the factors responsible for the geographical growth differences.

The decrease in stock size of many deepwater *Sebastes* spp. along the west coast of North America and the Gulf of Alaska may be related to the growth increase after about 1972 for both species. The major removals of this group by foreign fisheries occurred in the mid-1960's to 1970's (Bracken 1987; Ito et al. 1987; Westrheim 1987). Time series of reliable biomass estimates for *S. pinniger* and *S. diploproa* are not available, but estimates for *S. alutus* have been made using the stock reduction analysis method (Ito et al. 1987). All three species inhabit similar environments and depend upon similar food resources, so biomass estimates for *S. alutus* can be used as a proxy of biomass for the other two species. A comparison of the first principal component time series of *S. pinniger* and *S. diploproa* with the stock size of *S. alutus* on the west coast (Ito et al. 1987) shows that the increase in growth begins slightly after the major stock decline (Fig. 8). The stock size of *S. alutus* is negatively correlated with the first principal component (and thus growth indexes) for both species ($P < 0.01$).

If decreased stock size is responsible for the increased growth evident in both species, it apparently occurs in age groups 1–6 for *S. pinniger* (Figs. 3, 5A) and in age groups 2–6 for *S. diploproa* (Figs. 4, 5B). The ecological differences between age group 1 and older *S. diploproa* (described above) may explain why density-dependent growth does not occur in the young fish. Density-dependent growth in the first year of life has been described for several fishes (van der Veer 1986; Peterman and Bradford 1987) that

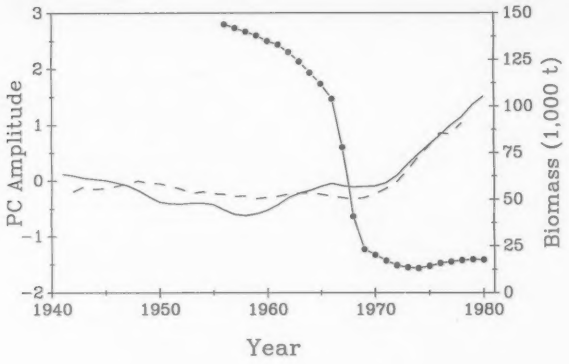

FIGURE 8.—Comparison of the smoothed first principal component time series of *Sebastes pinniger* (dashed line) and *S. diploproa* (solid line) with data on the stock size of *S. alutus* (circles) from Oregon, Washington, and British Columbia (Ito et al. 1987).

typically have a limiting juvenile habitat (often estuarine) and a much more extensive adult habitat. Indeed, Peterman and Bradford (1987) have suggested that density-dependent growth of English sole, *Parophrys vetulus*, off the coast of Oregon occurs only in the first year of life but not later. In *S. diploproa*, the opposite occurs. The adult habitat is restricted bathymetrically and latitudinally, whereas the pelagic prejuveniles occur in a very extensive epipelagic habitat subject to different environmental factors, competitors, and food resources. It is doubtful that variations in density of *Sebastes* in this habitat would impact growth significantly. In the adult habitat of both *S. pinniger* and *S. diploproa*, however, the immense virgin biomass of members of this genus has been reduced significantly. Further, most rockfish species commercially exploited by the trawl fishery rely on the same food resource, with euphausids as the principal prey (Phillips 1964; Brodeur and Pearcy 1984). The increased availability of prey resources associated with stock decline could conceivably result in increased growth in most species. Snytko and Fedorov (1974) suggested that some rockfish species have increased their geographic ranges at the expense of the decreased stocks of *S. alutus*; density-dependent growth could be a corollary of such a range extension.

The nonstationary characteristic due to the sudden increases in growth late in the time series makes correlations of growth indexes with environmental factors difficult to evaluate. Further, sea level, wind stress curl, and the first principal component time series of *S. diploproa* and *S. pinniger* were all serially correlated in the 1946–77 data base, indicating temporal trends that decrease the number of independent degrees of freedom in the sample correlation estimates and that introduce potentially spurious correlations (Chelton 1983, 1984; Bakun 1985). Correlations of the relationship of growth data to time series of physical factors (sea level, sea-surface temperature, upwelling index, and wind stress curl) were determined (Table 1); the 95% significance levels were calculated using the formula in Chelton (1983), which accounts for the reduced number of degrees of freedom from serial correlations. For *S. pinniger*, a significant, positive correlation existed between the second principal component and both the April-September upwelling index and sea level (Table 1); a significant, positive correlation also existed between both growth for age group 6 (G6 in Table 1) and the second principal component with the April-September upwelling index for the prior year. Growth in age group 6 contributed significantly to the variance described by the second principal component (Fig. 5A), so the similarity was not surprising. Feeding by *S. pinniger* increased during the spring-summer upwelling period when *Euphausia pacifica* was the dominant diet item and the frequency of empty stomachs was lower (Brodeur and Pearcy 1984). This must also be the time that fat deposition occurs in this species since the peak fat content was in fall (Guillemot et al. 1985). The effects of upwelling in a prior year on growth may be related to delayed growth using the energy from stored fat reserves built up during

the prior upwelling season. The importance of upwelling in rockfish feeding is shown by the decreased fat storage in El Niño years in *S. flavidus* (Lenarz and Echeverria 1986).

For *S. diploproa*, wind stress curl was negatively correlated with the growth indexes for age groups 2, 4, and 6, with mean growth for age groups 2–6 (G26), and with the first principal component (Table 1), which reflects most closely growth from ages 2–6 (Fig. 5B). Negative wind stress curl is associated with offshore convergence (Nelson 1977), which could concentrate prey (such as euphausids) and potentially increase feeding efficiency during the spring-summer upwelling season when maximum feeding takes place. Sea-surface temperature is negatively correlated with growth in year 2, whereas it is positively (but nonsignificantly) correlated with growth in year 1; the correlation between the second principal component (which reflects growth in year 1) and sea-surface temperature is significant, however, suggesting a real difference between the response of these age groups to temperature. This difference may be involved with an ontogenetic shift in the temperature for optimum growth for this species as noted by Boehlert (1981).

TABLE 1.—Pearson correlation matrices for six age group growth indexes (G1–6), mean growth indexes (G for *Sebastes pinniger*, G26 for *S. diploproa*), and principal component time series of the three dominant modes of variability (PC 1–3) with environmental factors from 1946 to 1977; mean yearly values (as opposed to smoothed values) are used in these calculations. The mean growth index for *S. diploproa* is for ages 2–6 because of differences in growth in age group 1. The significance levels of coefficients were calculated following Chelton (1983). CURL, wind stress curl at lat. 45°N, long. 125°W; UP, yearly average Bakun upwelling index at lat. 45°N; SSTNB, sea-surface temperature at Neah Bay, WA; UP49, upwelling index averaged for April–September; and SLSF, sea level at San Francisco.

Index	CURL	UP	SSTNB	UP49	SLSF
S. pinniger					
G1	−0.288	0.105	−0.254	0.163	−0.033
G2	0.065	−0.057	−0.032	−0.165	−0.236
G3	0.049	−0.296	−0.078	−0.261	−0.344
G4	−0.058	0.205	−0.173	−0.013	−0.182
G5	−0.066	0.162	−0.140	0.344	0.083
G6	−0.500	0.123	−0.088	0.274	0.429
G	−0.262	0.085	−0.243	0.127	−0.069
PC 1	−0.228	0.077	−0.247	0.109	−0.113
PC 2	−0.344	0.192	−0.061	0.416*	0.459*
PC 3	−0.178	0.261	−0.091	0.081	0.089
S. diploproa					
G1	0.007	0.034	0.363	−0.079	0.075
G2	−0.567*	−0.122	−0.351*	−0.025	−0.041
G3	−0.270	0.127	−0.072	0.062	0.277
G4	−0.453*	−0.392*	0.267	−0.326	−0.140
G5	−0.310	−0.024	−0.293	0.200	−0.216
G6	−0.349*	−0.056	−0.094	0.021	−0.350
G26	−0.619*	−0.163	−0.148	−0.027	−0.120
PC 1	−0.635*	−0.172	−0.145	−0.044	−0.130
PC 2	0.032	0.016	0.438*	−0.126	0.229
PC 3	−0.092	0.029	−0.175	0.200	−0.239

* = $P < 0.05$.

With the exception of the correlations noted above, the general lack of strong relationships of fish growth with physical parameters may be due to several causes. First, errors in methodology may cause lower resolution in the growth time series than would be necessary to demonstrate the associations. Second, the complexity of factors having an impact upon fish growth (Weatherley 1976; Brett 1979) makes detecting relationships of growth with individual physical factors difficult; furthermore, fish growth may be related to environmental factors in a nonlinear fashion. Higher resolution in the measuring technique and minimization of ageing errors will be necessary to address the first of these problems. The second problem can be addressed through nonlinear analysis of the relationships and continuation of the time series of growth anomalies, which will help define the relationships of growth with physical and biological factors.

CONCLUSION

The research we describe develops a new technique for constructing historical time series of fish growth and conducts analysis into the causes of growth variation in *Sebastes diploproa* and *S. pinniger*. The technique is applicable to a variety of marine organisms for which chronographic records are deposited in some calcareous structures. Our analysis of the record for *S. diploproa* and *S. pinniger* is characterized by a strong signal of increased growth late in the record. Although this signal is confounded by questions associated with size-selective mortality and Lee's phenomenon, we interpret it to indicate a density-dependent response to stocks depleted by overfishing. Our interpretation can be tested; if stocks of *Sebastes* are allowed to rebuild, the dominant signal of increased growth evident in the time series (Figs. 3, 4, 6, 7) should return to more normal values. We recommend that these time series be continued and that the techniques be applied to other species. The interrelationships among species and further investigation of the role of environmental factors in annual fish

growth variation could provide valuable insights into population responses of fishes to their physical and biological environment.

ACKNOWLEDGMENTS

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Interannual Trends in Pacific Cod, *Gadus macrocephalus*, Predation on Three Commercially Important Crab Species in the Eastern Bering Sea

Patricia A. Livingston

ABSTRACT: Pacific cod, *Gadus macrocephalus*, food habits data from 1981, 1984, and 1985 in the eastern Bering Sea were analyzed to determine interannual trends in consumption of three commercially important species of crabs: the red king crab, *Paralithodes camtschatica*, and two species of snow crabs, *Chionoecetes bairdi* and *C. opilio*. Soft-shell female red king crab were consumed during spring in Bristol Bay. Estimates of percentages of female red king crab standing stock consumed by the Pacific cod population were 3.8%, 2.8% and 1.4% in the respective sampling years of 1981, 1984, and 1985. This implied that Pacific cod were not the major force behind the observed decline in numbers of female red king crab in the population from 1981 to 1985. Predation mortality of *C. bairdi* by cod was estimated to be about 84%, 95%, and 94% of the population of age 1 crab during 1981, 1984, and 1985, respectively. Annual predation removal of age 1 *C. opilio* was 28%, 57%, and 27%, respectively, of the reconstructed population numbers of age 1 crab in the 3 years sampled. Although these calculations indicated that cod may consume large proportions of the age 1 snow crab populations, the estimates are tentative partly because of uncertainties in reconstructing the population numbers of age 1 crab.

The results also indicate that *C. bairdi* are more vulnerable to cod predation because of their high spatial overlap with cod populations, whereas an unknown fraction of the *C. opilio* juvenile population is north of the main survey area and does not overlap with cod. Results from this study suggest that predation by cod may be an important factor influencing survival of ages 1 and 2 snow crab in the eastern Bering Sea.

Pacific cod, *Gadus macrocephalus*, biomass in the eastern Bering Sea has increased by about 800,000 t over the last decade primarily because of two strong year classes spawned in 1978 and 1979. Stock biomass levels have been about 1 million metric tons since 1982 and a growing domestic fishery for this species is responsible for most of the catch (Thompson and Shimada 1987). Because Pacific cod are documented predators of soft-shell red king crab, *Paralithodes camtschatica*, and juvenile snow crab, *Chionoecetes opilio* and *C. bairdi*, (Mito 1974; Feder 1977; Jewett 1978; Blau 1986; Livingston et al. 1986), there has been an increase in speculation linking the decline of crab stocks with the increase in Pacific cod population size. The eastern Bering Sea red king crab population has decreased by an order of magnitude from a maximum of 365 million crab in 1977. Otto (1986) suggested reasons for the decline including weak year class production and large increases in natural mortality, which might be attributed to predation by Pacific cod, disease, or incidental catch in trawl fisheries. Pacific cod may also be implicated in the decline of red king crab abundance in the Kodiak region of the Gulf of Alaska (Blau 1986) and in the disappearance of certain year classes of *C. opilio* snow crab in the eastern Bering Sea (Incze and Schumacher 1986). Although circumstantial evidence has implicated Pacific cod predation in these crab population declines, direct evidence is so far lacking.

The regulation of prey population size by a predator requires that prey mortality rate increase with prey population size (direct density-dependent mortality, Holling 1959). Thus examination of changes in Pacific cod diet with changes in crab population abundance is necessary to determine whether the rate of cod predation on crab changes when crab abundance changes. Total removals of crab by cod need to be estimated and compared with crab population size. If percentage of removal of crab by cod alters with changes in crab density, then cod predation is a likely density-dependent factor regulating crab population size.

I examined the interannual trends in Pacific cod predation on three commercially important crab species in the estern Bering Sea: red king crab, *C. opilio*, and *C. bairdi*. Three years of Pacific cod food habits data from 1981, 1984, and 1985 were analyzed to determine 1) the areas

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where crab predation occurred, and whether this changed with time in response to environmental variables; 2) changes in the percentage by weight and size distribution of crab in the diet by year; and 3) total amounts of crab consumed by the Pacific cod population for each year calculated from food habits data, daily ration, and Pacific cod population abundance estimates. Estimated removals of crab by Pacific cod for each year were compared with the size distribution and population levels of crab estimated from annual research surveys to determine whether cod exerted density-dependent control over crab population size.

METHODS

Sample Collection and Laboratory Analysis

Stomachs were collected from 4,023 Pacific cod (30–107 cm fork length (FL)) during the three years (1981, 1984, and 1985) in the eastern Bering Sea (Fig. 1, Table 1). Samples were taken from May through September using bottom trawl gear on research and commercial fishing vessels. Sampling occurred throughout the 24 h day in 1984 and 1985 and from 0600 to 2000 Alaska daylight time in 1981. Stomachs were removed at sea and placed in cloth bags labelled with information regarding the location of capture and the length, sex, and sexual maturity of the fish. Individual fish weights were calculated using a length-weight relationship developed for Pacific cod in the eastern Bering Sea (Bakkala et al. 1986). Fish showing evidence of regurgitation (i.e., food in the mouth or throat, or a flaccid stomach) were not included in the sample. Stomachs were preserved in 10% formalin and later transferred to 70% ethyl alcohol. Contents were identified to the lowest taxonomic level possible and enumerated. Wet weights were recorded after the contents were blotted with paper towels. If carapaces were intact, snow crabs in the stomachs were measured to the nearest millimeter carapace width (CW), and king crabs were measured to the nearest millimeter carapace length (CL).

Data Analysis

Pacific cod were divided into two size groups for data analysis: 30–59 cm FL and ≥60 cm FL. Previous studies (Livingston et al. 1986) show that cod become increasingly piscivorous beyond 60 cm FL, and mean stomach content weight as a percentage of body weight is also much larger for cod ≥60 cm in length. Thus, the food habits and daily ration need to be examined separately for the two size groups of cod.

Logistic regression, using the BMDPLR routine in the BMDP statistical software package (Dixon 1983), was performed to determine which major factors (predator size and year) were important in describing variation in predation by cod on a particular crab species. The dependent variable was the presence or absence of a crab species in cod stomachs from two cod size groups (Size 1 = 30–59 cm, Size 2 = ≥60 cm) during the three sampling years (1981, 1984, and 1985). The most parsimonious model was chosen for describing predation on each crab species using the criteria that 1) only factors that resulted in a significant improvement ($P < 0.05$) in model fit be added and, 2) the overall model goodness of fit chi-square be nonsignificant ($P > 0.05$), indicating that the model provided a good fit to the data. In addition, BMDPLR permitted

TABLE 1.—Stomach sample collection information of Pacific cod taken in 1981, 1984, and 1985 in the eastern Bering Sea.

Year	Sampling dates	Number of hauls	Sampling times (ADT)[1]	Number of stomachs			Sampling platform
				30–59 cm	≥60 cm	Total	
1981	5/23–8/3	145	0600-2000	1,130	527	1,657	research vessels
1984	5/9–9/29	157	0000-2359	560	410	970	research vessels foreign commercial vessels
1985	5/5–9/30	148	0000-2359	870	706	1,576	research vessels foreign commercial vessels

[1]ADT is Alaska daylight time.

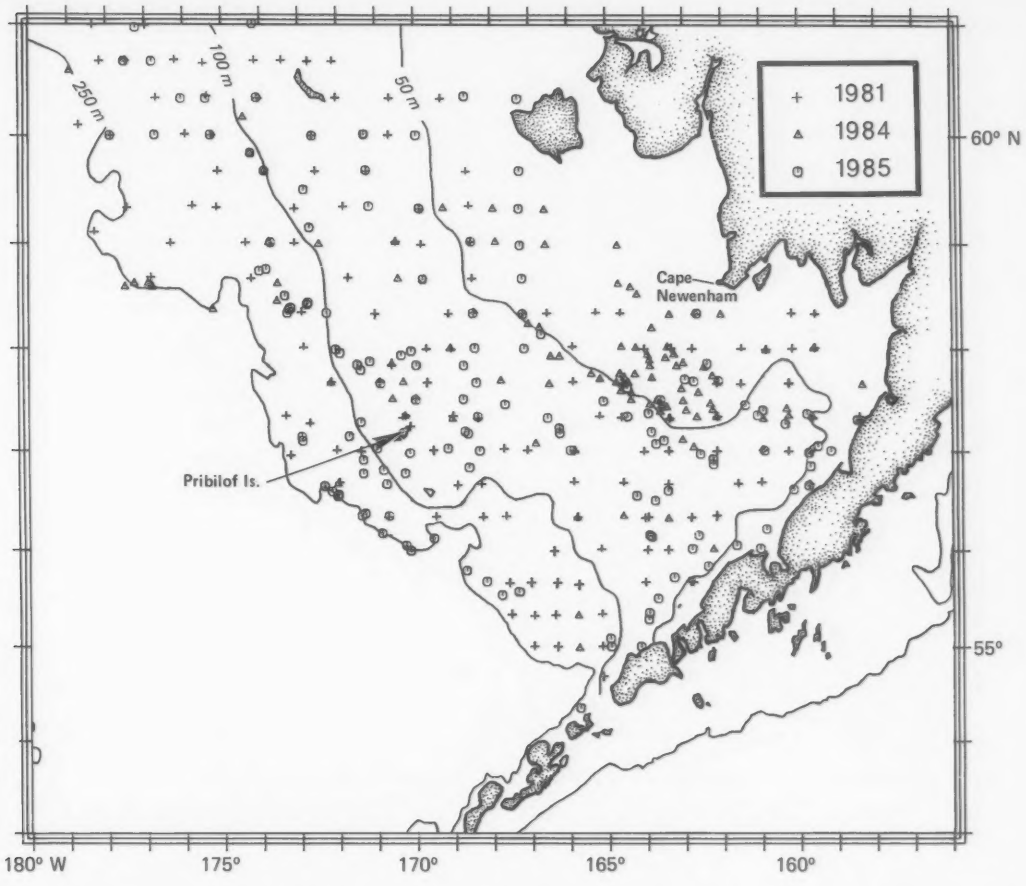


FIGURE 1.—Haul locations where Pacific cod, *Gadus macrocephalus*, stomach samples were taken during 1981, 1984, and 1985 in the eastern Bering Sea.

significance tests of the relationship between levels of each factor, so that a description of which predator sizes and sampling years had higher occurrences of crab predation could be presented.

Estimates of the total amount of each crab species consumed by the Pacific cod population during the sampling period for each year was calculated according to Mehl and Westgard (1983):

$$C_i = DR_i \cdot D \cdot B_i \cdot P_i \qquad (1)$$

where C_i is the consumption (by weight) of crab by cod belonging to size group i, DR_i is the daily ration (as a proportion of body weight daily, BWD) of cod size group i, D is the number of days in the sampling period of May through September when crab were vulnerable to predation, B_i is the biomass of cod size group i, and P_i is the proportion (by weight) of the crab species in the diet of cod size group i.

The areas of crab consumption by cod were derived by plotting the areal distribution of the percentage by weight of each species of crab in the diet for each year. A polygon encompassing the area where each species of crab was consumed was obtained for each year. The percentage by weight of a crab species in the diet of each size group of cod (P) was calculated solely from stomachs taken inside the crab consumption area. To eliminate spatial sampling bias (i.e., samples unevenly distributed within a crab consumption area), the percentage by weight of crab in the diet was calculated by taking the average of the percentages for each 20 nmi wide

square where stomachs were sampled within a crab consumption area. Since cod sometimes consume only the legs of red king crab, these stomachs were not included in the estimation of P because this behavior may not contribute to predation mortality.

Because recent studies indicate that individual prey size or weight is a more important factor influencing gastric evacuation rates in fish than prey type (Ursin et al. 1985; Jobling 1987), Pacific cod daily ration (R) was calculated using mean stomach content weight (S) in grams for each year and cod size group in the following equations from Ursin et al. (1985). These equations describe daily ration for Atlantic cod, *Gadus morhua* (whose diet and morphology are very similar to Pacific cod), as a function of mean individual prey weight (w) in grams, and bottom temperature (T) in °C:

$$R = aS \qquad (2)$$

where $a = a_0\, w^{a_1}$ and $a_0 = a_{00}\, e^{0.096T}$ and where $a_0 = 0.61\ d^{-1}$, $a_{00} = 0.33$, and $a_1 = -0.36$ for North Sea temperatures were adjusted for the Bering Sea using the average bottom temperature for Pacific cod stations sampled in each year from expendable bathythermographs obtained at most stations.

The number of days (D) when snow crab were vulnerable to predation was considered to be the whole sampling period of May through September (153 days) because predation on hard-shell juveniles of both species has been shown to occur throughout this period (Livingston et al. 1986). Although the Pacific cod's diet contains large amounts of snow crab during other times of year, geographic distribution of samples taken in other periods was not sufficient to include in the current study. Because red king crab in the hard-shell state are very spiny, cod probably consume adults only when they are in the soft-shell state. During the period sampled in this study, only female red king crab are molting (males molt earlier in the year), and their molt extends only through May of the study period ($D = 30$).

Pacific cod biomass was estimated using data collected simultaneously with stomach collections during resource assessment surveys conducted each year by the Resource Assessment and Conservation Engineering (RACE) Division of the Northwest and Alaska Fisheries Center (NWAFC). The catch per unit of effort (CPUE) of cod in kg/nmi^2 was calculated using the area swept method for each 20 nmi wide square where resource assessment trawls were performed in each crab consumption area. The cod CPUE was then separated into the CPUE for each cod size group using the length-frequency information from resource assessment surveys. Total biomass for each cod size group could then be calculated as the sum of the CPUEs multiplied by the area of 20 nmi wide square (400 nmi^2).

Population estimates and size distributions of crab from assessment surveys were provided by Robert Otto[1]. Population assessment methods for crab are described in Otto (1986).

Although size-at-age determinations are uncertain for snow crab, crab were separated into age classes using the following carapace width-at-age tables for *C. opilio* and *C. bairdi* commonly used by crab biologists at the NWAFC (J. Reeves[2]).

	Carapace width (mm)	
Age	*C. opilio*	*C. bairdi*
0	<5	<9
1	5–24	9–34
2	25–39	35–49
3	40–59	50–69
4	60–74	70–84
5	75–94	85–104
6+	≥95	≥105

Ice edge locations were taken from ice edge atlases (Joint Ice Center 1981, 1984, and 1985). These data come principally from satellite imagery. In each year, I chose the last observed southernmost ice edge extent during spring before the permanent ice retreat.

RESULTS

Geographic Distribution of Crab Consumption by Year

In all three years, red king crab were consumed by cod in the crab consumption area bounded by long. 165°00′W in the west and lat. 58°30′N at depths of 31–100 m (Fig. 2). Red king crab were found in stomachs from May through

[1]R. Otto, Kodiak Laboratory, RACE, Northwest Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Kodiak, AK 99615, pers. commun. 1986.

[2]J. Reeves, Northwest Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98115, pers. commun. May 1988.

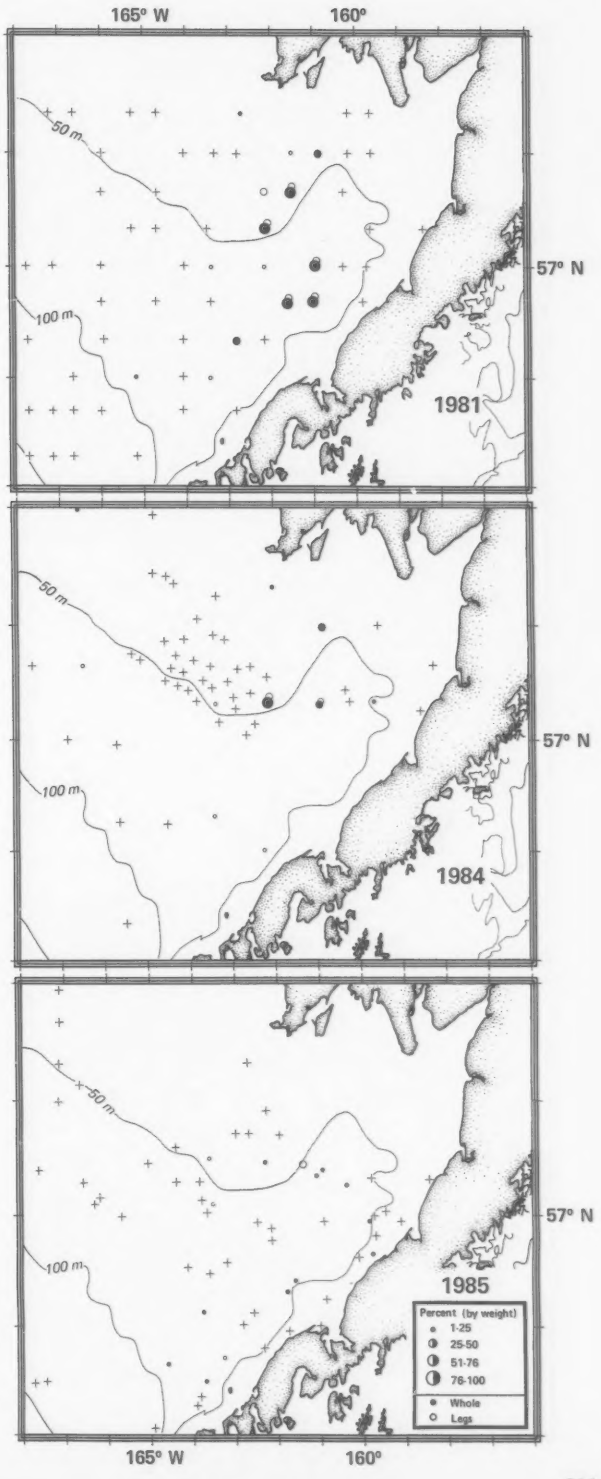


FIGURE 2.—Percentage by weight of red king crab, *Paralithodes camtschatica*, in Pacific cod stomachs by geographic location in 1981, 1984, and 1985. (Open circles denote percentage by weight of red king crab legs and black circles denote percentage by weight of whole red king crab. +'s are locations where cod were sampled but no red king crab were eaten.)

July. There was no noticeable trend over years with regard to areas where legs were consumed versus areas where whole red king crab were eaten. The percentage by weight of legs in the diet of cod at each station was generally less than 25% for all 3 years. The percentage of whole king crab eaten at each station seemed to decrease from 1981 to 1985.

The geographic distribution of *C. opilio* and *C. bairdi* in Pacific cod stomachs during 1981, 1984, and 1985 are shown in Figure 3. The figure also shows the approximate ice edge location before the final ice retreat for each year. In 1981, small percentages (<25% by weight) of *C. bairdi* were found in Pacific cod stomachs around the Pribilof Islands and also at bottom depths of 50–100 m in the area southeast of the Pribilofs. In contrast, this species was consumed over a much broader area of the southeastern Bering Sea shelf during 1984 and 1985. *Chionoecetes bairdi* also appeared in stomach contents of cod caught near the shelf edge at 200 m, even in areas northwest of the Pribilof Islands. This species was encountered in stomach contents throughout the sampling period of May through September.

In general, consumption of *C. opilio* did not overlap much geographically with the areas where *C. bairdi* were consumed, except near the Pribilof Islands. Most *C. opilio* were eaten north of the Pribilof Islands in a broad band encompassing depths from 35 to 200 m, although the highest percentages by weight in Pacific cod stomachs seemed to be in the middle shelf area with bottom depths of 50–100 m. In 1981, high percentages by weight of *C. opilio* appeared in cod diet north of 59°00′N, corresponding with the location of the ice edge before its retreat in that year. While the southward extension of predation appeared to go down to 57°30′N in 1984, the percentages by weight in the diet were not as high as in 1981. In 1985, cod diets were composed of fairly high percentages by weight of *C. opilio* as far south as 56°30′N; the ice edge in that year was at approximately the same latitude.

Differences in Diet Composition Within Areas by Year and Cod Size

Results of logistic regression of the frequencies of occurrence for each crab species in the two Pacific cod size groups for 1981, 1984, and 1985 are presented in Table 2. The most significant relationship for describing Pacific cod consumption of whole red king crab was Pacific cod size: cod larger than 60 cm contained whole red king crab more frequently than cod 30–59 cm in length. Interannual differences in frequency of occurrence of red king crab in stomachs were also significant, showing a decrease in occurrence from 1981 to 1985. Percentages by weight and frequency of occurrence of red king crab in cod stomachs followed similar year and size trends (Fig. 4).

TABLE 2.—Results from logistic regression of frequencies of occurrence of each crab species against year (1981, 1984, and 1985) and Pacific cod size group (Size 1 = 30–59 cm, Size 2 = ≥60 cm).

Crab species	Main factors chosen[1]	df	Improvement: Chi-square	Improvement: *P* value	Relationship among factor levels[2]
Paralithodes camtschatica	Size	1	29.549	0.000	Size 2 > Size 1
	Year	2	11.960	0.003	1981 > 1984 ≥ 1985
	Residual (goodness of fit)	2	(3.578)	(0.167)	
Chionoecetes bairdi	Size	1	14.832	0.000	Size 1 > Size 2
	Residual (goodness of fit)	4	(23.378)	(0.000)[3]	
C. opilio	Year	2	81.699	0.000	1985 > 1984 > 1981
	Size	1	10.341	0.001	Size 2 > Size 1
	Residual (goodness of fit)	2	(2.379)	(0.304)	

[1]Main factors chosen ($P < 0.05$) are shown in order of entry into the model.
[2]Determined from significance and sign of between-level contrasts.
[3]Chosen model has poor fit due to one anomalous cell: Size 2 in 1981 had much lower frequency of occurrence of *C. bairdi* than other cells. (Year was not significant.)

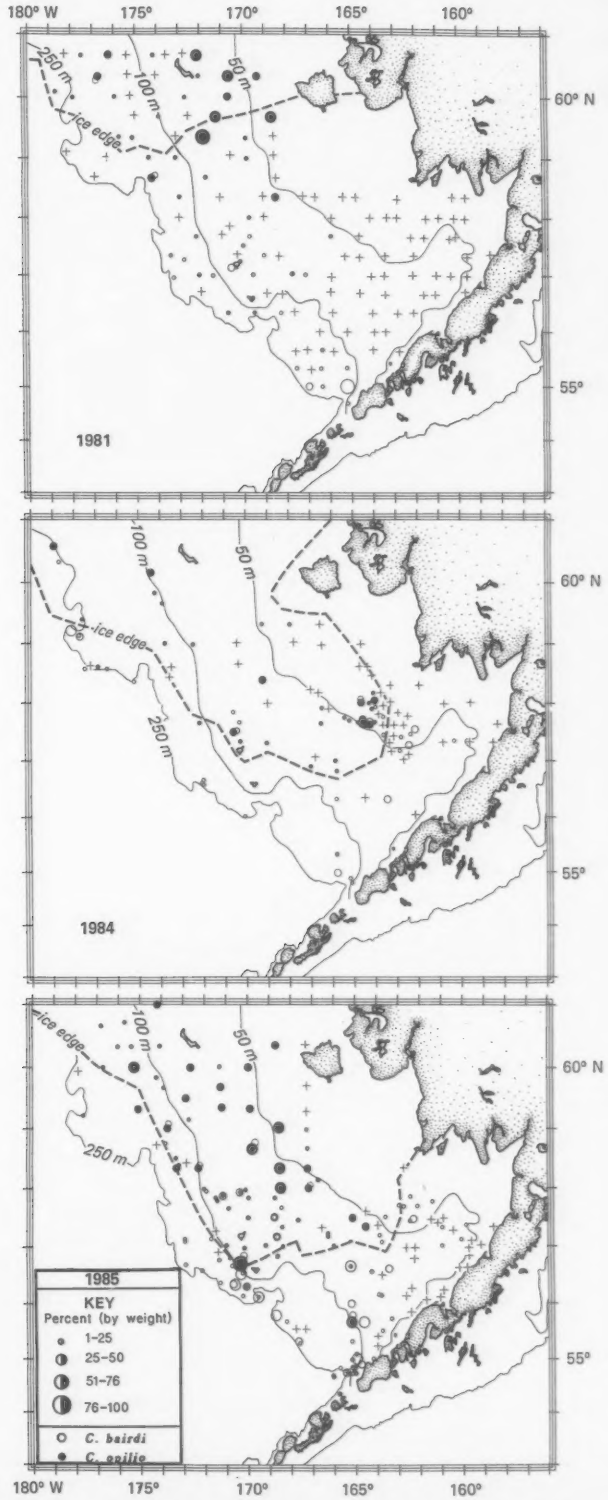


FIGURE 3.—Percentage by weight of *Chionoecetes bairdi* (open circles) and *C. opilio* (black circles) in Pacific cod stomachs by geographic location in relation to the ice edge before its last retreat in 1981, 1984, and 1985.

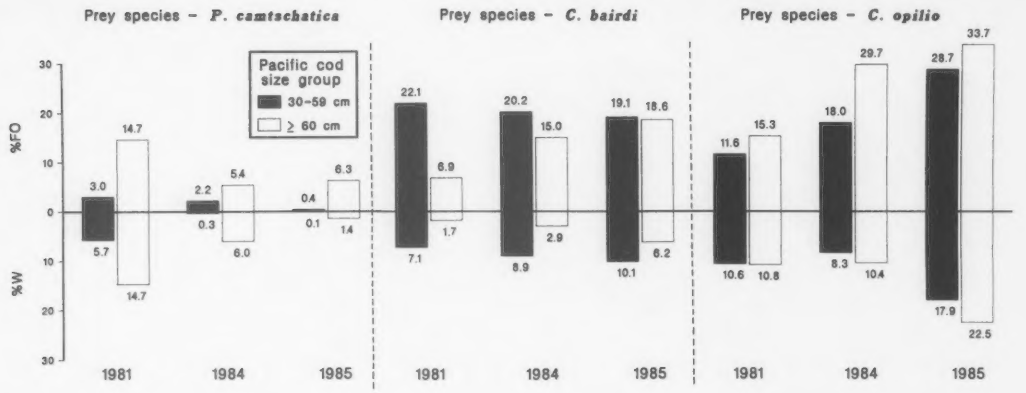


FIGURE 4.—Percentage of frequency of occurrence (%FO) and percentage by weight (%W) of red king crab, *Paralithodes camtschatica*, and two species of snow crab, *Chionoecetes bairdi* and *C. opilio*, in stomachs of two Pacific cod size groups in the respective crab consumption area during 1981, 1984, and 1985.

The only significant relationship for the occurrence of *C. bairdi* was fish size; cod 30–59 cm in length contained this crab species more frequently than cod ≥60 cm. The chosen model fits these data poorly because of the presence of one anomalous cell; cod ≥60 cm in 1981 contained *C. bairdi* much less frequently than any other group. The anomalous value produces a size-year interaction wherein small cod do not show interannual differences in the occurrence of *C. bairdi*, while large cod seem to have an increase in occurrence over time. The percentages by weight also show a size-related difference in *C. bairdi* consumption.

Year was the most important variable describing differences in occurrence of *C. opilio* in cod stomachs; occurrence increased from 1981 to 1985. Size was also significant, with large cod consuming this species more frequently than did small cod. Percentages by weight of *C. opilio* do not show the same trends as strongly as do the frequency of occurrence data; 1981 and 1984 appear similar and the size-related differences do not look as strong.

Size Frequencies and Sex Ratios of Crab Species

Only 10 red king crab CL measurements were taken over all three years because of the advanced state of digestion of most of these crabs found in Pacific cod stomachs. Carapace lengths ranged from 53 to 160 mm with an average of 106 mm. Nine out of 10 crabs were larger than 90 mm. Sex was determined for only one specimen; it was a female.

The Kolmogorov-Smirnov test (Zar 1974) showed that there was no significant difference ($P > 0.05$) between *C. bairdi* size distributions (Fig. 5) consumed by cod 30–59 cm in 1984 and 1985, and no significant size difference between *C. bairdi* consumed by cod ≥60 cm in 1981, 1984, and 1985. All other size-frequency distribution comparisons, in particular comparisons between cod size groups within years, showed significant differences. Most *C. bairdi* in smaller cod (30–59 cm) were <20 mm CW, while large cod consumed crab in the 20–30 mm CW size range. Size distributions of crab <95 mm CW from survey results show size-frequency modes at 40 mm CW or greater. In 1981, most crab in the survey were >60 mm CW.

The only size-frequency distributions of *C. opilio* (Fig. 6) that were not significantly different ($P > 0.05$) from each other were those for smaller cod (30–59 cm) in 1984 and 1985. The size distributions of *C. opilio* consumed during 1981 by both cod size groups were very different from size distributions for the other 2 years. Smaller cod during that year ate more crabs larger than 30 mm CW than in other years, and the modal crab size consumed by large cod (≥60) was also greater (40–50 mm CW) compared to 1984 and 1985. Crab size distributions from the survey show size frequency modes at 40–50 mm CW.

The proportions of female snow crabs in Pacific cod stomachs and in resource assessment trawl surveys were determined (Table 3). In cod stom-

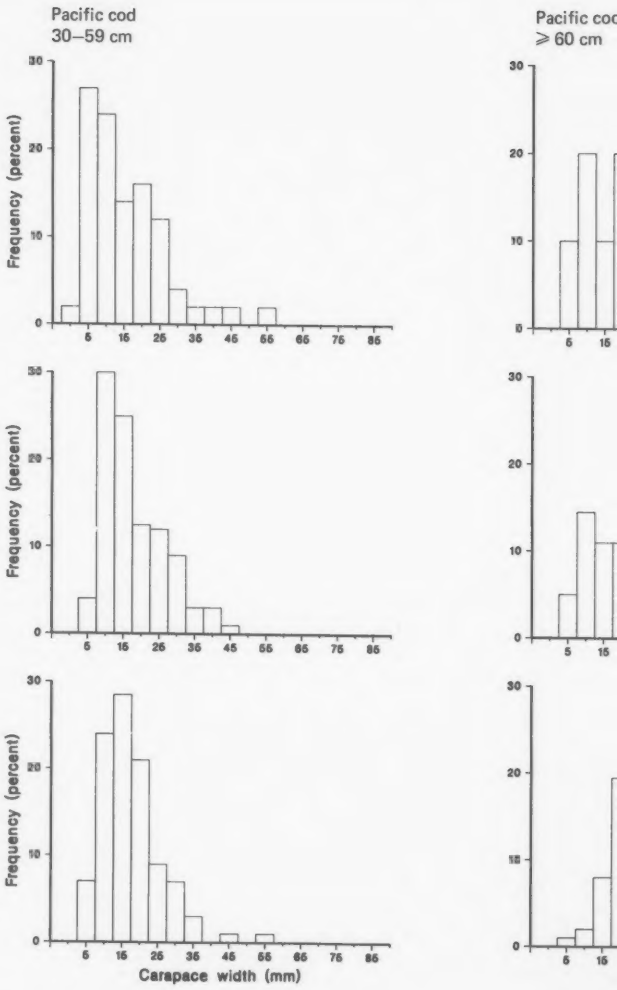
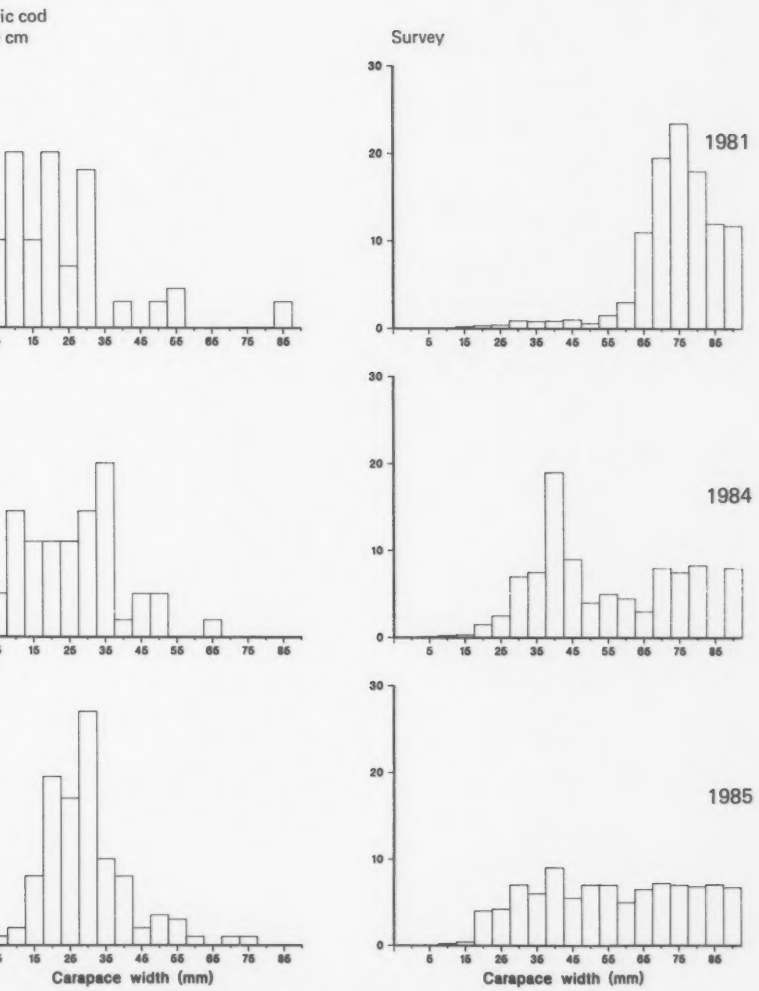


FIGURE 5.—Relative size-frequency distribution of *Chionoecetes bairdi*
during 1



bairdi in stomachs of two Pacific cod size groups and in the resource assessment survey
uring 1981, 1984, and 1985.

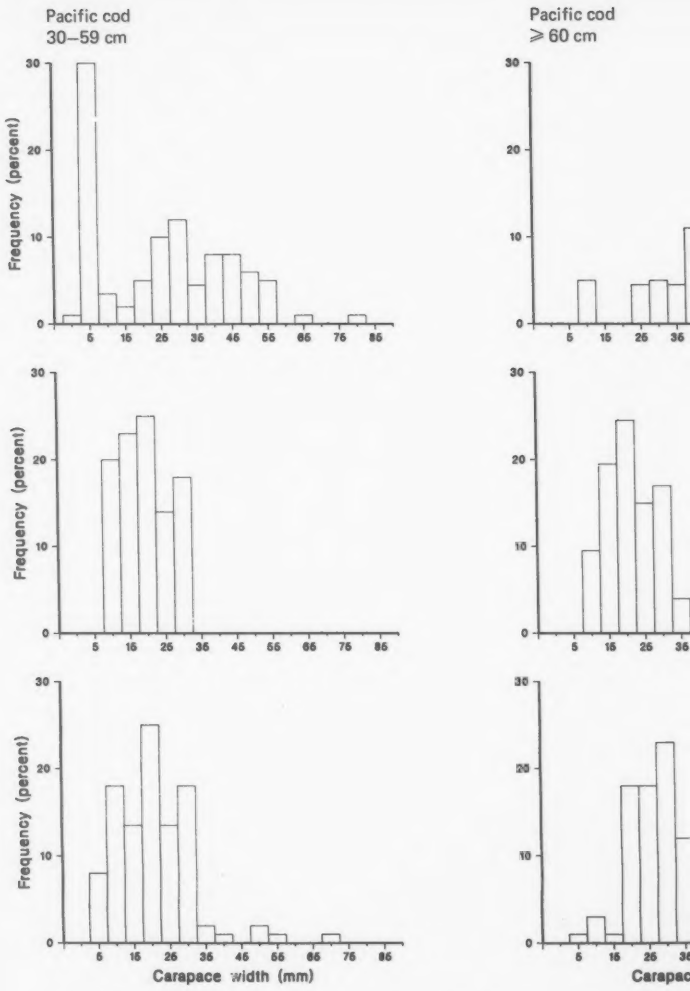
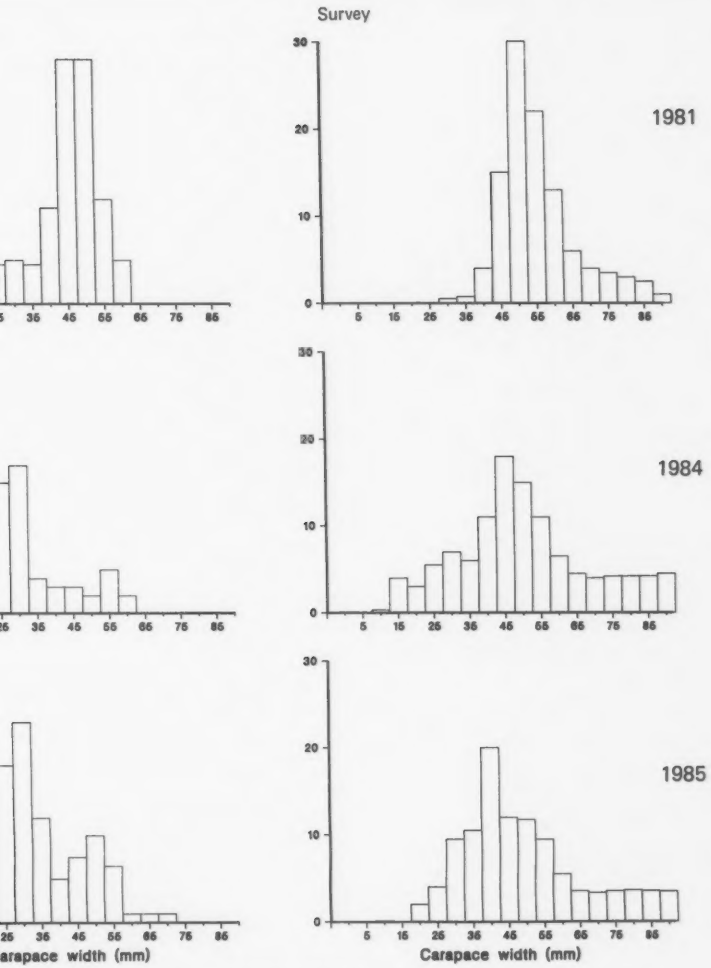


FIGURE 6.—Relative size-frequency distribution of *Chionoecetes opilio* in ston
during 1981, 198



n stomachs of two Pacific cod size groups and in the resource assessment survey
81, 1984, and 1985.

TABLE 3.—Total number (*N*) and proportion of female snow crabs (PF), *Chionoecetes bairdi* and *C. opilio*, in Pacific cod stomachs and resource assessment trawl surveys for the years 1981, 1984, and 1985 in the eastern Bering Sea.

		Stomachs		Survey[1]	
Crab species	Year	*N*	PF	*N*	PF
C. bairdi	1981	248	[2]0.935	6,774	0.675
	1984	180	[3]0.567	5,770	0.645
	1985	817	0.557	2,664	0.567
C. opilio	1981	77	[2]0.857	22,728	0.640
	1984	165	[3]0.557	19,709	0.510
	1985	512	0.607	12,125	0.426

[1]Sex ratios and number of crab sexed provided by Resource Assessment and Conservation Engineering Division, Kodiak Laboratory for crab <95 mm CW.
[2]Crab sex was not consistently recorded by stomach analysts during this year.
[3]Observed proportion was not significantly different from 0.5 ($P > 0.05$) using the normal approximation to the binomial test.

achs, the proportions of females for both species of snow crabs during 1981 were much larger than other years. In 1984 and 1985, the proportions of females in cod stomachs were fairly close to 0.5, although in the normal approximation to the binomial test (Zar 1974) only the proportions in 1984 were not significantly different ($P > 0.05$) from 0.5; a test of an even sex ratio. Trawl survey estimates of the proportion of female snow crab <95 mm CW range from 0.43 to 0.67. In some cases the proportion of females observed in stomach contents differed from the proportion estimated from the trawl survey. No trends seem readily apparent except that trawl survey estimated proportions, and those proportions in Pacific cod stomach contents were more similar in 1984 and 1985 than during 1981.

Pacific Cod Population Consumption of Crab

Daily ration estimates range from about 0.5 to 0.9% BWD with small cod consuming larger rations as a percentage of their body weight than large cod in a given year (Table 4). Rations for both cod groups were smaller in 1985 than in 1981 and 1984 because of the lower bottom temperature and the large individual prey weight for large cod in that year.

The parameters necessary for calculating population consumption are the cod biomass in the prey area, the percentages by weight of each crab species in the diet, and the number of days the crab species is vulnerable to cod predation (Tables 5–7). The calculations for the total amount of red king crab consumed by cod assume that only female crabs are consumed, and the period of predation vulnerability during the sampling period is 30 days in May when female crabs are in the soft-shell condition. Further, because of the small number of crabs measured from stomach contents in each year, the average carapace length of all red king crab measured in a year was used to calculate the total number of crab consumed (1981 = 104 mm CL and 1984–85 = 111 mm CL; corresponding to about age 6 for females).

Both total biomass and numbers of red king crab consumed by cod declined from 1981 to 1985 by a factor of 10 (Table 5). The total amount of *C. bairdi* consumed by cod during the 153 d sampling period in each year, in terms of total weight and numbers, decreased slightly from 1981 to 1984 and increased about threefold from 1984 to 1985 (Table 6). Although the total biomass of *C. opilio* consumed by cod dropped dur-

TABLE 4.—Parameters used to derive daily ration estimates and the estimated daily rations for two size groups of Pacific cod in 1981, 1984, and 1985 in the eastern Bering Sea. (% BWD is percentage of body weight daily.)

		Average weight (g)			Bottom	
Year	Cod size group	Cod	Individual prey	Cod stomachs	temperature (°C)	Daily ration (% BWD)
1981	30–59	1,340	1.02	25.1	3.7	0.86
	≥60	4,045	12.31	141.4	3.7	0.66
1984	30–59	1,095	0.48	16.7	3.1	0.87
	≥60	4,994	6.55	180.7	3.1	0.80
1985	30–59	1,217	1.00	18.7	2.3	0.63
	≥60	5,383	18.67	180.0	2.3	0.47

TABLE 5.—Parameters used to obtain cod population consumption estimates for *Paralithodes camtschatica* and the estimated total biomass and numbers consumed by the cod population. (Assuming this species of crab is vulnerable to cod predation for only 30 days of the study period.)

Year	Cod size (cm)	Cod biomass (1,000 t)	Percent crab in diet (by weight)	Total biomass crab consumed (1,000 t)	Total number crab consumed (millions)
1981	30–59	118	5.7	1.7	2.00
	≥60	39	14.7	1.1	2.00
			Total	2.8	4.00
1984	30–59	72	0.3	0.1	0.06
	≥60	127	6.0	1.8	2.00
			Total	1.9	2.06
1985	30–59	89	0	—	—
	≥60	103	1.4	0.2	0.20
			Total	0.2	0.20

TABLE 6.—Parameters used to obtain cod population consumption estimates for *Chionoecetes bairdi* and the estimated total biomass and numbers consumed by the cod population. (Assuming this species of crab is vulnerable to cod predation during the whole 153 days of the study period.)

Year	Cod size (cm)	Cod biomass (1,000 t)	Daily ration (%BWD)	Percent crab in diet (by weight)	Total biomass crab consumed (1,000 t)	Total number crab consumed (billions)
1981	30–59	122	0.86	7.1	11.4	2.71
	≥60	140	0.66	1.7	2.4	0.10
				Total	13.8	2.81
1984	30–59	51	0.87	8.9	6.0	0.91
	≥60	164	0.80	2.9	5.8	0.31
				Total	11.8	1.22
1985	30–59	224	0.63	10.1	21.8	3.87
	≥60	246	0.47	6.2	11.0	0.51
				Total	32.8	4.38

TABLE 7.—Parameters used to obtain cod population consumption estimates for *Chionoecetes opilio* and the estimated total biomass and numbers consumed by the cod population. (Assuming this species of crab is vulnerable to cod predation during the whole 153 days of the study period.)

Year	Cod size (cm)	Cod biomass (1,000 t)	Daily ration (%BWD)	Percent crab in diet (by weight)	Total biomass crab consumed (1,000 t)	Total number crab consumed (billions)
1981	30–59	274	0.86	10.6	38.2	1.72
	≥60	136	0.66	10.8	14.8	0.28
				Total	53.0	2.00
1984	30–59	100	0.87	8.3	11.0	2.00
	≥60	164	0.80	10.4	20.9	1.29
				Total	31.9	3.29
1985	30–59	185	0.63	17.9	31.9	4.06
	≥60	173	0.47	22.5	28.0	1.03
				Total	59.9	5.09

ing 1984 compared with 1981 and 1985, the total number of crab consumed increased over the whole time period, reflecting the smaller sizes of crab consumed in 1984 and 1985 (Table 7).

Total numbers by age of *C. bairdi* and *C. opilio* consumed are shown in Figures 7 and 8. Most *C. bairdi* consumed are age 1, but ages 0, 2, and 3 are also represented. This figure does not show the small amount (3 million) of age 5 crab eaten in 1981 or the 5 million age 4 crab eaten during 1985. Cod consumption of *C. opilio* is mainly directed at crab of ages 1–2. More *C. opilio* of ages 3–4 are eaten than *C. bairdi*.

DISCUSSION

The geographic distribution of Pacific cod predation on red king crab corresponds to the main area of red king crab abundance from NMFS resource assessment trawl surveys. These surveys produce relatively precise abundance estimates for crab >75 mm CL (Otto 1986) which is

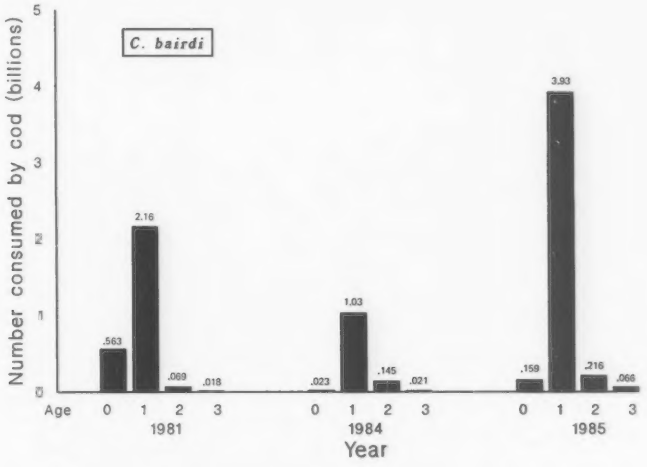


FIGURE 7.—Total number by age group of *Chionoecetes bairdi* consumed by the Pacific cod population in 1981, 1984, and 1985.

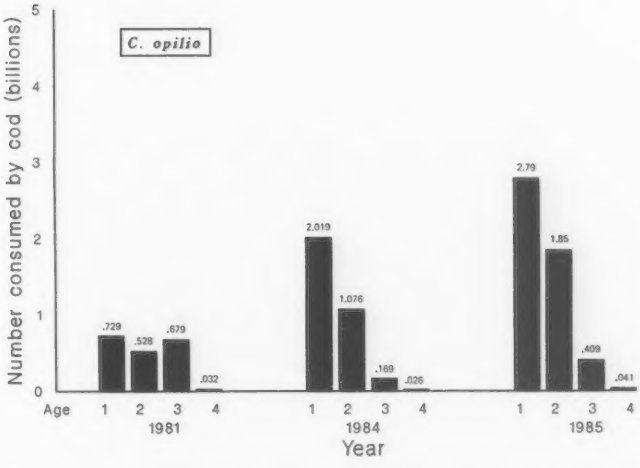


FIGURE 8.—Total number by age group of *Chionoecetes opilio* consumed by the Pacific cod population in 1981, 1984, and 1985.

the size range of red king crab consumed by cod in this study. However, the areas of cod predation on snow crab show interannual variation that does not match areas of adult abundance determined from NMFS trawl surveys, probably because the trawls used in these surveys do not catch small snow crabs <40 mm CW, which is the size consumed most by cod. Surveys showed most adult *C. bairdi* to be east and southeast of the Pribilof Islands in 1981, 1984, and 1985, while cod stomach contents showed no small *C. bairdi* east of 165°00'W in 1981. Similarly, surveys showed high densities of *C. opilio* >95 mm CW as far south as the Pribilofs in 1981, whereas most small *C. opilio* eaten by cod were much farther north in that year.

The geographic distribution of snow crab predation by Pacific cod was very different in 1981 than in the other two years, and the more northerly location of the ice edge in that year relative to 1984 and 1985 suggests an environmental relationship between *C. opilio* distribution and physical factors. Somerton (1981, 1982) postulated a direct relationship between spring ice cover and planktonic larval survival of *C. opilio* in order to explain observed high recruitment to the adult population of those year classes that may have been in the plankton and benefited from the associated ice edge production during 1971 and 1972 in the eastern Bering Sea. Instead of a relationship between ice cover and planktonic survival, however, our data suggest that ice cover in a given year may also indicate the areal extent of juvenile *C. opilio* in the same year. Since benthic dwelling juveniles would not benefit directly from an ice edge bloom, the ice edge in a particular year may be an indicator of another environmental variable such as bottom temperature.

The average bottom temperature at stations where *C. opilio* were found in cod stomachs is compared (*t*-test) with bottom temperatures where no *C. opilio* were consumed during the three years of this study (Fig. 9). The average bottom temperatures (≤3°C) were significantly lower ($P < 0.05$) for the locations where *C. opilio* were found than for locations where they were absent. Somerton (1981) reported the weighted average bottom temperatures at stations where *C. opilio* occurred in 1979 was less than 3°C when the weights used were crab abundance. In that year, juveniles <40 mm CW had the highest abundances per station, indicating that the temperatures apply mainly to the juvenile portion of the population. In the northwest Atlantic, Brêthes et al. (1987) found bottom temperatures <3°C to be the most significant factor in determining the spatial distribution of juvenile *C. opilio* <40 mm CW in the Gulf of St. Lawrence. Thus, the geographic distribution of juvenile *C. opilio* appears to depend mostly on bottom temperature; highest densities are found in areas where bottom temperatures are less than 3°C and those areas may be a significant portion

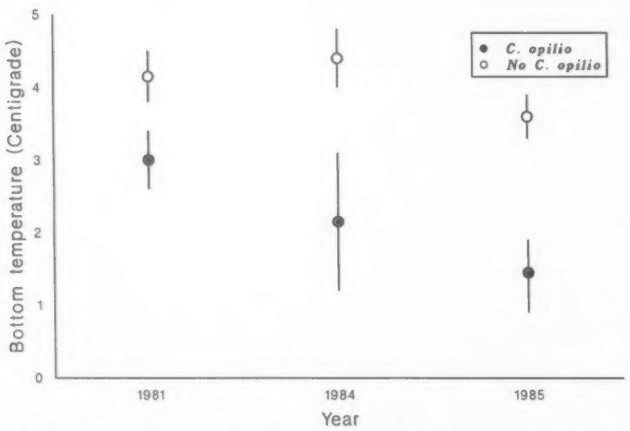


FIGURE 9.—Mean bottom temperature (°C) and 95% confidence intervals at locations where Pacific cod consumed *Chionoecetes opilio* (black circles) and at locations where Pacific cod did not contain *C. opilio* (open circles) in 1981, 1984, and 1985.

of the eastern Bering Sea shelf in cooler years.

Diet Composition by Year and Cod Size

Analysis of frequencies of occurrence of red king crab in Pacific cod stomachs through logistic regression shows that cod size is the most important factor in determining consumption of whole red king crab; the frequency of occurrence was significantly greater in cod larger than 60 cm FL. Blau (1986) found that Pacific cod, which presumably had consumed soft-shell female king crabs in the Kodiak region of the Gulf of Alaska, ranged in size from 45 to 79 cm FL. That study, however, did not examine differences in frequency of occurrence within that size range, and none of the crab eaten were whole. Interannual differences in red king crab consumption were significant in our study, decreasing from 1981 to 1985. NWAFC abundance estimates for the female portion of the red king crab population show a corresponding trend with a decrease in numbers from 103.6 million in 1981 to 13.7 million in 1985. This suggests that individual cod predators responded to decreases in crab density by consuming less crab.

Although logistic regression of *C. bairdi* frequencies of occurrence showed cod size as an important variable, the model fit was poor due to the low frequency of crab occurrence in cod ≥60 cm FL in 1981. If the percentages by weight are examined (Fig. 4), the size relationship looks clearer. Smaller cod consistently ate more than large cod, and the interannual changes within size groups showed consistent, small increases across years. NMFS surveys are not able to provide precise estimates of crab <40 mm CW, not only because of escapement through trawl meshes, but also because snow crab <100 mm CW have a greater tendency to bury themselves in bottom sediments (Conan and Maynard 1987), reducing their vulnerability to trawl capture. If cod respond to changes in *C. bairdi* density as they appear to do for red king crab density, then our data suggest the possibility of stable or slight increases in juvenile *C. bairdi* population numbers for crab <40 mm CW over the three study years. The similarity of *C. bairdi* size distributions in cod stomachs for the three years within each cod size group further supports the suggestion of stable juvenile (<40 mm CW) *C. bairdi* population size distributions over time.

The model which best explains *C. opilio* consumption by cod shows year as the most important variable (with consumption increasing over years) and size as the next important variable (with larger cod consuming *C. opilio* more frequently than smaller cod). If the occurrence of juvenile crab <40 mm CW in cod diets can be used as a measure of juvenile crab abundance in the survey area, then our data show a probable increase in juvenile *C. opilio* abundance from 1981 to 1985. Waiwood and Elner (1982) similarly suggested that the increase in Atlantic cod, *Gadus morhua*, predation on snow crab observed in 1980 and 1981 in the Gulf of St. Lawrence in the northwest Atlantic was due to increased availability of small crabs. The size-frequency distributions of *C. opilio* in cod stomachs also indicate more *C. opilio* <35 mm CW in 1984 and 1985 than in 1981 at least in the survey area. Somerton (1981) showed that large numbers of *C. opilio* juveniles exist north of 61°00′N, an area which was not sampled in this study. It is possible that in colder years such as 1984 and 1985, an influx of juvenile *C. opilio* from these northern areas could have entered southeastern Bering Sea shelf waters and have become more available to cod. Of course, there is a limit to the distance juvenile crab can migrate in one year. The observed downward shift in mean size and increased numbers of *C. opilio* in cod stomachs may not be the result of actual increases in juvenile *C. opilio* abundance but might be the result of progressive southerly shifts in the geographic distribution of small juveniles in progressively colder years. More years of data need to be examined, however, to determine what happens to juvenile distributions over time, particularly between two consecutive years with very different climatic conditions.

Because of the large carapace lengths of red king crab consumed by cod (50–160 mm CL), the well-digested nature of red king crab in stomachs, the usual occurrence of whole crab only around May, and the fact that one red king crab's sex was determined to be female, we have assumed that Pacific cod consume soft-shell females, which molt in Bristol Bay around April to May (Hayes 1983). It seems highly unlikely that cod could consume whole crab of those carapace lengths in a hard-shell condition. Blau (1986) also found cod consuming red king crab during the king crab molting period in the Gulf of Alaska. Because male red king crab molt in winter while migrating to the mating grounds (Powell and Nickerson 1965), our assumption that only soft-shell females are consumed in spring seems supportable. This does not rule out the possibility that cod may consume soft-shell males, which

molt during winter. However, our winter sampling coverage has been limited and has not detected this type of occurrence.

With the exception of 1981, when stomach analysts did not consistently record snow crab sex, the proportions of female juvenile snow crabs in stomach contents were close to 0.5 and were not significantly different from a 1:1 ratio of females to males in 1984. Adams (1979) reviewed the literature on *C. opilio* and found that the early life history of males and females are similar with respect to size, growth, distribution, and habitat. Brêthes et al. (1987) found sex ratios of *C. opilio* <30 mm CW in the northwest Atlantic to be 1:1 with no spatial segregation of sexes. The proportions of female snow crabs <95 mm CW in the NMFS assessment surveys were close to 0.5 in most years. Thus, cod do not appear to be selecting snow crab on the basis of sex and are probably preying randomly on individuals on the basis of crab size.

Pacific Cod Population Consumption of Crab

Daily rations that were derived using the Ursin et al. (1985) model for incorporating prey size effects on gastric evacuation rate appear reasonable compared with estimates of daily ration for Atlantic cod from areas with bottom temperatures higher than temperatures in the eastern Bering Sea. My estimates ranged from 0.47 to 0.86% BWD; and estimates for Atlantic cod of similar sizes range from 0.5 to 1.0% BWD in the North Sea (Daan 1973), 1.6 to 2.0% BWD in the Faroe plateau (Jones 1978), and 0.5 to 1.9% BWD on Georges Bank (Durbin et al. 1983). Livingston et al. (1986) calculated daily ration for Pacific cod using the Elliott and Persson (1978) model without correction for prey size effects using a subset of the data presented in this paper and obtained values of 0.31% BWD for cod <55 cm FL and 1.30% BWD for cod >55 cm FL. When compared with cod growth data, however, the rations for small cod were too small to account for growth, and rations for large cod were too large. The current approach seems to correct for the deficiencies in the previous estimates, and produces ration values which are not so divergent for the two cod size groups.

Other parameters involved in estimating population consumption are also subject to error: predator biomass estimates, the percentage of prey items in the predator's diet, and the number of days the crab species is vulnerable to predation. NMFS survey estimates of cod biomass in recent years have 95% confidence intervals of 12–18% of the mean biomass estimate (Thompson and Shimada 1987), a minimum confidence interval because of the assumptions of complete vulnerability and catchability of cod to bottom trawls. Cod also performed seasonal onshore-offshore migrations (Wespestad and Shimada 1984); a factor not taken into consideration here that could change the biomass of cod in a particular area over the time period in this study. Errors in diet composition parameters can arise from insufficient sample sizes, uneven spatial distribution of samples, and possible diet changes over space and time scales not considered in this study. Sampling effort for cod stomachs was widely distributed over the whole shelf area during 1981 and 1985, but some areas were not sampled well during 1984 (Fig. 1). I have attempted to reduce bias in diet composition estimates that may arise from uneven stomach sample sizes within areas by averaging diet percentages estimated for each 20 nmi wide square where stomachs were sampled within a crab consumption area. A similar practice has been adopted in the North Sea stomach sampling program, which provides diet composition estimates for a multispecies virtual population analysis model (Mehl 1986). In this study, I have estimated consumption that occurred only during May through September, so the estimated numbers of snow crab consumed by cod apply only to that portion of the year. Livingston et al. (1986) has shown that Pacific cod in the eastern Bering Sea consume snow crab throughout the whole year; therefore, the estimates presented in this paper can be considered mainly as indexes of the total numbers consumed by cod. There is also great uncertainty about the size at age for crabs and the allocation of crab size groups to age classes should be considered approximate.

Impact on Crab Populations

Predation mortality rate of a prey population must increase with prey population size in order to demonstrate that a predator population is regulating the size of the prey population (Holling 1959). NMFS resource assessment surveys provide annual estimates of female red king crab abundance, which can be compared with the total cod population removals of female red king crab in the same year (Fig. 10). Both the female red king crab population and the estimated removals from the population by cod follow the

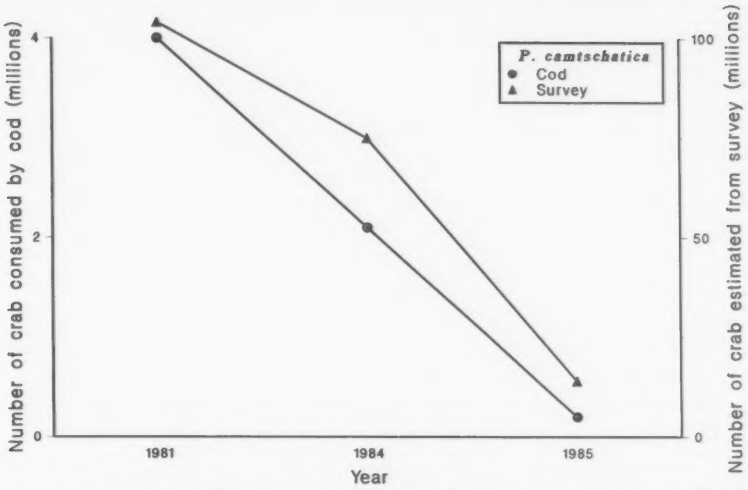


FIGURE 10.—Total number of red king crab, *Paralithodes camtschatica*, eaten by the Pacific cod population during 1981, 1984, and 1985 compared with resource assessment estimates of the total female red king crab population during the same years. (Note different y-axis scales.)

same pattern of linear decline. Removals, expressed as a percentage of the population, are 3.8%, 2.8%, and 1.4% for the years 1981, 1984, and 1985, respectively. The declining percentages removed actually indicate weak compensatory density-dependent mortality over time, which appears to be mainly due to the functional response of individual cod to declining prey populations (i.e., a decline in the average amount of crab per predator with a decline in crab population). Thus, at least over the range of female red king crab population sizes considered here, it appears that cod predation is not responsible for the observed declines in female red king crab populations from 1981 to 1985. The percentages removed by cod form a small and declining part of the total population decline. Since the period of red king crab vulnerability to cod predation for the present study included only 30 out of a possible 60 days when red king crab females are in the soft-shell condition, the estimated removals could be doubled to approximate total annual amounts removed by cod. This would affect the percentage of removals in each year by a factor of two but would not change the seemingly compensatory density-dependent relationship between crab removals and crab population size.

A similar comparison cannot be made directly for cod consumption of the two snow crab species because cod consume mostly age 1 crab, which are not well estimated in NMFS research surveys. However, the numbers of age 1 snow crab eaten in a particular year can be compared to the number of age 3 crab collected 2 years later in NMFS research surveys, which should be more precise (Figs. 11, 12). Although the curves of age 1 crab consumed and the number of age 3 crab found 2 years later in the trawl surveys appear to be somewhat similar in shape for *C. bairdi* for the 3 years, the estimated numbers of age 1 crab consumed in a particular year are about two orders of magnitude greater than the numbers of age 3 crab found 2 years later. This at least indicates that cod are responsible for removing large numbers of age 1 crab relative to the number that remain at age 3. The unequal ratios of prey removed to prey remaining among years could also indicate that density-dependent removals are occurring.

The numbers of age 1 crab in the population can be reconstructed, as in Forney (1977), by adding the number remaining at age 3 to the number of age 1 eaten by cod. This assumes that cod predation is the major source of mortality for crab less than age 3 and that virtually all of this mortality occurs at age 1. If removals by cod are calculated as a percentage of the reconstructed population size, then the values obtained for 1981, 1984, and 1985 are 84%, 95%, and 94%, respectively. These percentages are substantial

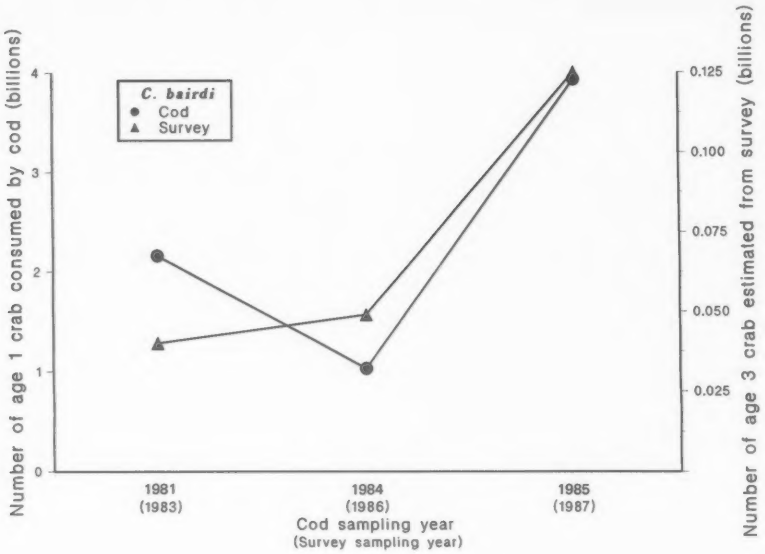


FIGURE 11.—Total number of age 1 *Chionoecetes bairdi* snow crab eaten by the Pacific cod population during 1981, 1984, and 1985 compared with resource assessment estimates of the age 3 population in 1983, 1986, and 1987. (Note different y-axis scales.)

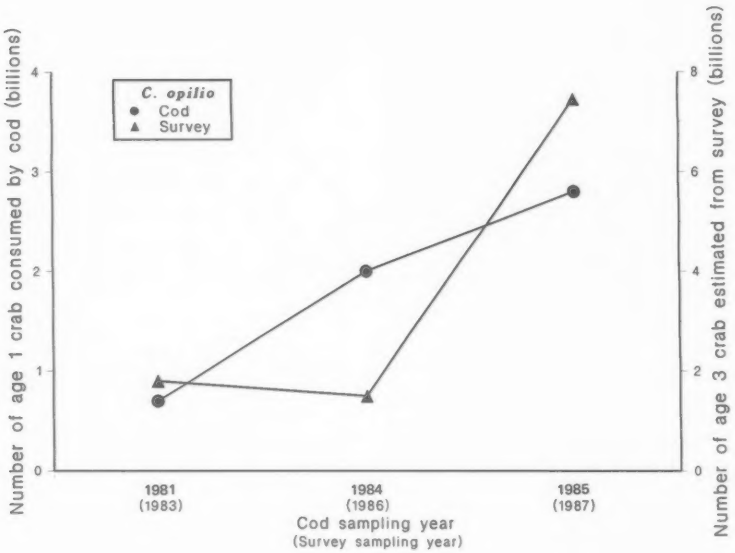


FIGURE 12.—Total number of age 1 *Chionoecetes opilio* snow crab eaten by the Pacific cod population during 1981, 1984, and 1985 compared with NWAFC resource assessment estimates of the age 3 population in 1983, 1986, and 1987. (Note different y-axis scales.)

portions of the estimated age 1 population and could be an indication of overestimation of the population consumption by cod, underestimation of the age 1 population size because of unaccounted sources of mortality or underestimation of age 3 numbers by research trawl surveys. As mentioned earlier, cod have been shown to consume snow crab throughout the year in the eastern Bering Sea so the current estimate of 153 days for vulnerability to predation by cod is an underestimate. Further, the cod diet contained fair amounts of snow crab that could not be identified to the species level due to state of digestion and were not included in the estimates. This again leads to conservative estimates of the total number of snow crab consumed by cod.

A similar comparison of *C. opilio* removals at age 1 by cod with trawl survey estimates of numbers remaining at age 3 shows that numbers remaining at age 3 are greater than those eaten at age 1 during 1981 and 1985. Percentages removed of the reconstructed age 1 cohort would be 28%, 57%, and 27% for 1981, 1984, and 1985, respectively. These percentages are overestimates because substantial numbers of age 2 *C. opilio* are also eaten (Fig. 8) but not included in the reconstructed population estimate.

Although these estimates are subject to many sources of error, the high predation mortality rates of juvenile crab found here may not be unrealistic. Using food habits data to quantify predation removals, multispecies virtual population analysis of North Sea fish stocks produced average annual instantaneous predation mortality coefficients ranging from 0.2 to 1.8 for age 1 fish in the model (Daan 1987). Large interannual differences in predation mortality coefficients were observed within fish species, suggesting that predator populations were exerting density-dependent control on some year classes. Similarly, our study has shown the possibility of large predation removals of mostly age 1 snow crabs and some interannual variation in the percentages removed. The impact on *C. bairdi* seems greater than on *C. opilio*, at least for age 1 crab. *Chionoecetes bairdi* are also more vulnerable to cod predation because of their high spatial overlap with cod populations. In contrast, unknown portions of the *C. opilio* juvenile population are north of the main survey area, and the main center of their distribution may shift south into areas populated by cod in some years.

Analysis of a longer time series of cod predation data may help locate abundant crab year classes and allow us to track their numbers over time. There is uncertainty about the growth patterns of juvenile snow crabs, and following size class modes in cod stomach data in succeeding years may provide more clues to these growth patterns. Further, although this study does not attempt to explain factors influencing early life history survival, it does suggest that predation is an important factor influencing survival of ages 1 and 2 snow crab.

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A Comparative Analysis of Growth Zones in Four Calcified Structures of Pacific Blue Marlin, *Makaira nigricans*

Kevin T. Hill, Gregor M. Cailliet, and Richard L. Radtke

ABSTRACT: Sagittae, vertebrae, and anal and dorsal fin spines collected from Pacific blue marlin in Kona, Hawaii were evaluated for legibility and interpretability of growth patterns, ease of collection and processing, and the precision of the resultant annulus counts for use in estimating age. Sagittae, and anal and dorsal fin spine sections contained growth zones assumed to be annual events and there was a linear relationship between age estimates of corresponding samples. Vertebrae had numerous minute growth increments, but contained no marks which could be interpreted as annual. While nonparametric tests revealed no significant difference between age estimates from different hardparts of the same fish, dorsal and anal spine counts had the best agreement. Anal and dorsal fin spines were more practical in terms of ease of collection, processing, legibility, and interpretation; however, age estimates of spine samples from larger fish required a statistical replacement of inner growth zones that were destroyed by matrix expansion. Although more difficult to collect and interpret, sagittae provide more detailed age information. Mean length-at-estimated age data based on anal spine band counts are also presented.

Increased knowledge of billfish age and growth is essential for sensible management of these fisheries. Although there is a paucity of such information for most billfish species, the Western Pacific Fisheries Management Council was forced to draft a management plan for the Pacific blue marlin, *Makaira nigricans*, with only cursory data (WPFMC 1985). This lack of information is due to the many difficulties involved with studies of large pelagic fish species (Prince and Pulos 1983), compounded by lack of routine sampling programs by research agencies in the Pacific region.

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Various calcified structures have been utilized for age estimation of the Istiophoridae. Dorsal spine sections have provided age estimate data for Atlantic sailfish, *Istiophorus platypterus* (Jolley 1974, 1977; Hedgepeth and Jolley 1983), Atlantic white marlin, *Tetrapterus albidus*, and Atlantic blue marlin, *Makaira nigricans* (Prince et al. 1984). Sagittal otoliths have been described as potentially useful structures for ageing most billfish species (Radtke 1981, 1983; Radtke and Dean 1981; Radtke et al. 1982; Prince et al. 1984; Wilson 1984; Cyr 1987). Jolley (1974) described numerous circuli in the vertebrae of sailfish; however, both scales and vertebrae have now been dismissed as structures for age estimation in billfish (Prince et al. 1984).

Age estimation of Pacific blue marlin is still in the developmental stages, and most data have focused on sagittae (Radtke 1981; Wilson 1984), with little effort on other skeletal structures. The objective of the present study was to examine, interpret, and quantitatively compare growth patterns in the sagitta, vertebrae, and dorsal and anal fin spines of blue marlin from Kona, HI. Each structure was evaluated in terms of ease of collection and processing, legibility of growth patterns, and the relative precision of the resulting age estimates.

MATERIALS AND METHODS

Pacific blue marlin were sampled at the Hawaiian International Billfishing Tournaments in Augusts 1982 (n = 48), 1983 (n = 113), and 1984 (n = 98), and at the Kona Gold Jackpot tournament in May 1983 (n = 20), Kailua-Kona, HI. Additional spine samples were obtained from the Pacific Gamefish Research Foundation (n = 32), the Hawaii Fishing Agency (n = 2), and the National Marine Fisheries Service, Southeast Fisheries Center (a specimen from Kona which was shipped to Miami for taxidermy). Meristic data collected for each fish included lower jaw-fork length (LJFL to 0.1 cm),

roundweight (W to 0.5 lb converted to kg), sex, and date of capture (Hill 1986).

Anal and Dorsal Fin Spine Analyses

Anal and dorsal fin spines were collected and prepared for analysis following modified methods of Prince et al. (1984) (Hill 1986). The second anal spine and sixth dorsal spine were selected for age analysis. These were chosen because they were the thickest of the spine complex, and sections taken from spines anterior to these had more prominent core matrices.

Spine length, defined as the distance from the hole at the center of the condyle base to the spine tip, was measured to the nearest millimeter. Thin cross sections from anal and dorsal fin spines were taken at positions marked at 10% and 5% (respectively) of the spine length from the condyle hole. Spine sections were examined using a compound stereoscope at 63× and 120× magnification using either transmitted light or reflected light with a black background. The focus of the spine was defined as the midpoint of the distance between the anterior and posterior portions of the spine along the midsagittal plane. All growth bands were counted and their radii measured with an ocular micrometer along the plane from the focus of the spine to the widest radius of the spine section. Spine radius (anal spine radius = AR; dorsal spine radius = DR) was defined as the distance from the focus to the outside edge of the spine along the same plane.

Statistical replacement of early missing anal and dorsal spine growth bands in larger fish was accomplished by summarizing band radii statistics from smaller, younger specimens in which these early bands were visible. Compiled band radius statistics included spine samples which had at least the first or second band visible. Unpaired *t*-tests were applied to compare corresponding radii between those specimens containing the first and second band and to compare corresponding band radii between sexes.

Final corrected age estimates were assigned to spine samples missing early bands by comparing the radii of the first four visible bands to the means and 95% confidence limits of the compiled data. When the radii of at least three successive bands of the first four visible bands fitted well within the 95% confidence limits of three or four bands of the compiled data, corresponding ages were assigned. The use of this technique to provide final age estimates was based upon the assumption that there was a predictable number of growth bands per millimeter of radius in the core matrix, and that the first several visible bands were analogous in age to matching bands of the compiled radius data.

Sagitta Analyses

Sagitta were cleaned, prepared, and examined following the methods of Radtke (1983) and Hill (1986). Terminology for sagitta orientations is based on Prince et al. (1986). Sagittal otolith weight (SW) was measured to the nearest 0.005 mg. Age assignments were based on combined counts of external growth features present on the sagittae, which included ridges along the anterior rostrum edge on the ventral plane of growth and ridges along the ventral surface of the medioventral and medial planes of growth.

Previous studies of Istiophorid sagitta have supplemented age estimates based on external features with examination of internal growth features using thin transverse sections and light microscopy (Wilson 1984; Prince et al. 1986). However, Hill (1986) statistically compared age estimates using external and internal growth features and found no significant difference between the two methods. Therefore, age estimates reported in this study were based only upon examination of external features.

Vertebrae Analyses

Caudal vertebrae numbers 22 and 23 were removed from the area between the posterior portion of the second dorsal fin and the base of the caudal fin. These were the only vertebrae which could be removed without lowering the market value of the fish. Vertebrae were simmered for several hours in hot water to remove extraneous tissues and then air dried for at least 72 hours. Vertebral spines and arches were removed, anterior and posterior centra separated, cut longitudinally along the dorsoventral plane, and stored in 95% isopropyl alcohol.

Vertebral cone depth (CD) (as defined by Johnson 1983), referred to in this paper as centrum cone depth was measured to the nearest 0.05 mm. Growth rings were observed after carefully peeling away the thin layer of cartilaginous tissue which covers the bony face of the centra. Centrum length, from focus to outside edge, was divided into approximately 5 mm sections and the average number of rings per millimeter was calculated for each section by counting three 1 mm portions in each section. Total

increment number was extrapolated from these data.

Assessment of Ageing Techniques

The usefulness of each hardpart for estimating age in blue marlin was assessed by considering ease of collection, hardpart growth, precision of age estimates, and the legibility of each hardpart.

To test the hypothesis that hardpart growth was proportional to somatic growth of the animals, both LJFL and W were modeled with AR, DR, SW, and CD, categorized by sex. The significance (two-tailed test) of r^2 values was tested (Schefler 1979). A paradigm of the ageing theory is that the number of increments in or on a hardpart increases with the growth of the structure. To test this assumption, AR, DR, SW, and CD were modeled against increment counts for each structure and the significance of the r^2 values was tested.

Relative precision of age estimates and hardpart legibility were determined by comparing the variability of estimated ages between hardparts from the same fish. Direct comparisons of age estimates from corresponding hardparts (anal spines, dorsal spines, and sagittae) were modeled with linear regression, and the slopes of these regressions were tested to see if they varied significantly from parity (Ho: beta = 1; Zar 1984). The significance of correlation coefficients (r) of the comparisons was tested using methods outlined by Schefler (1979). These relationships were also tested using a Wilcoxon Signed Ranks test (Sokal and Rohlf 1981). Owing to the difference in increment types, vertebrae were not considered in these comparisons.

To test the consistency of age estimates within and between readers, a subsample of 20 of each hardpart was read three times each by two readers. Age estimates were compared using the Average Percent Error (APE) method of Beamish and Fournier (1981). Mean age estimates of each of these comparisons were compared using the Wilcoxon Signed Ranks test. Uncorrected anal and dorsal spine band counts were utilized for all reader comparisons.

RESULTS

Hardparts and morphometric data were taken from a total of 211 male and 105 female blue marlin. Males ranged in size from 114.8 cm LJFL (19.1 kg) to 263.1 cm LJFL (170.3 kg) and females from 147.0 cm LJFL (20.9 kg) to 445.8 cm LJFL (748.0 kg). The 263.1 cm LJFL male and the 445.8 cm LJFL female are the largest specimens of blue marlin from which biological data have been reported in the literature. The mean length of females (264.9 cm LJFL) was significantly greater than that of males (205.1 cm

TABLE 1.—Summary of numbers and size ranges of Pacific *Makaira nigricans* from which skeletal hardparts and measurements were collected. LJFL = lower jaw-fork length, AR = anal spine radius, DR = dorsal spine radius, SW = sagittal otolith weight, CD = centrum cone depth.

		LJFL (cm)			Weight (kg)			Hardpart size	
Hardpart	N	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Anal spines								AR (mm):	
Males	150	114.8	263.1	205.3	19.1	170.3	75.0	3.98	10.10
Females	49	163.8	363.4	260.4	35.2	555.2	180.8	5.66	18.11
Dorsal spines								DR (mm):	
Males	66	177.0	263.1	208.7	46.3	170.3	78.5	7.65	12.46
Females	30	163.8	445.8	275.7	35.2	748.0	227.4	6.58	21.00
Otoliths								SW (mm):	
Males	54	169.5	251.5	206.4	38.6	138.8	75.9	0.415	4.985
Females	45	163.8	445.8	265.9	35.2	748.0	197.4	0.800	10.400
Vertebrae								CD (mm):	
Males	122	169.5	251.5	206.3	38.6	138.8	74.8	17.45	40.48
Females	77	147.0	337.7	261.1	20.9	447.7	176.5	18.30	45.99
Total									
Males		114.8	263.1	205.1	19.1	170.3	74.2		
Females		147.0	445.8	264.9	20.9	747.9	190.9		

LJFL) (Student's t-test; $P < 0.05$). Not all hardparts were collected from all fish. For a breakdown of fish size ranges and hardparts collected, the reader is referred to Table 1.

Hardpart Growth

The relationships between AR, DR, and CD, and LJFL were best described by significant ($P < 0.001$) positive linear equations (Table 2). Coefficient of determination values ranged from $r^2 = 0.19$ for male vertebrae to $r^2 = 0.72$ for female anal spines (Fig. 1). The relationships between SW and LJFL were exponential, with $r^2 = 0.41$ for males and $r^2 = 0.35$ for females (Table 2, Fig. 2). Logarithmic equations best described the relationships between AR, DR, CD, and W for both sexes (Table 2). Coefficient of determination values were significant ($P < 0.001$), ranging from $r^2 = 0.30$ for male vertebrae to $r^2 = 0.87$ for female dorsal spines. Sagitta weight had a linear relationship with W, with $r^2 = 0.32$ for males and $r^2 = 0.46$ for females.

Overall, there were generally higher coefficients of determination between AR, DR, CD, and W compared with those with LJFL. In addition, females generally had stronger relationships between hardpart size and body size (LJFL and W) when compared to males, the exception to this being the relationship between female SW and LJFL.

Growth Increments

Thin cross sections of dorsal and anal fin spines revealed a vascularized core matrix and a cortical region containing major growth bands (Fig. 3). A growth band was composed of alternations of translucent and opaque rings. Many growth bands were comprised of smaller rings that were most obvious at the widest lateral portion of the spine section (Fig. 4). Since band radii were measured from the focus outward along the widest portion of the spine, excessive numbers of smaller rings along the counting path made delineation of the outside edge of the translucent zone difficult at times, especially in exceptionally large spine samples. In such cases, it was necessary to refer to the dorsal and ven-

TABLE 2—Modeled relationships between fish growth (in length and weight) and hardpart growth for male and female Pacific *Makaira nigricans*. LJFL = lower jaw-fork length, W = roundweight, AR = anal spine radius, DR = dorsal spine radius, SW = sagitta weight, CD = centrum cone depth.

Comparison	Equation	r^2 value
Anal spine radius vs. LJFL		
Males	$AR = -0.5207 + 0.0394(LJFL)$	0.52
Females	$AR = -2.5879 + 0.0528(LJFL)$	0.72
Anal spine radius vs. W		
Males	$AR = 1.3061 * W^{0.4079}$	0.62
Females	$AR = 1.5300 * W^{0.3885}$	0.81
Dorsal spine radius vs. LJFL		
Males	$DR = -0.2700 + 0.0474(LJFL)$	0.49
Females	$DR = 0.2440 + 0.0526(LJFL)$	0.71
Dorsal spine radius vs. W		
Males	$DR = 2.0850 * W^{0.3513}$	0.53
Females	$DR = 2.3157 * W^{0.3499}$	0.87
Sagittal weight vs. LJFL		
Males	$SW = 0.0152 * 10^{(0.0103 * LJFL)}$	0.41
Females	$SW = 0.3250 * 10^{(0.0038 * LJFL)}$	0.35
Sagittal weight vs. W		
Males	$SW = -0.642 + 0.0412(W)$	0.32
Females	$SW = 1.1625 + 0.0144(W)$	0.46
Vertebral cone depth vs. LJFL		
Males	$CD = 2.5616 + 0.1226(LJFL)$	0.19
Females	$CD = 5.2871 + 0.1106(LJFL)$	0.45
Vetebral cone depth vs. W		
Males	$CD = 7.509 * W^{0.3031}$	0.30
Females	$CD = 10.101 * W^{0.2377}$	0.50

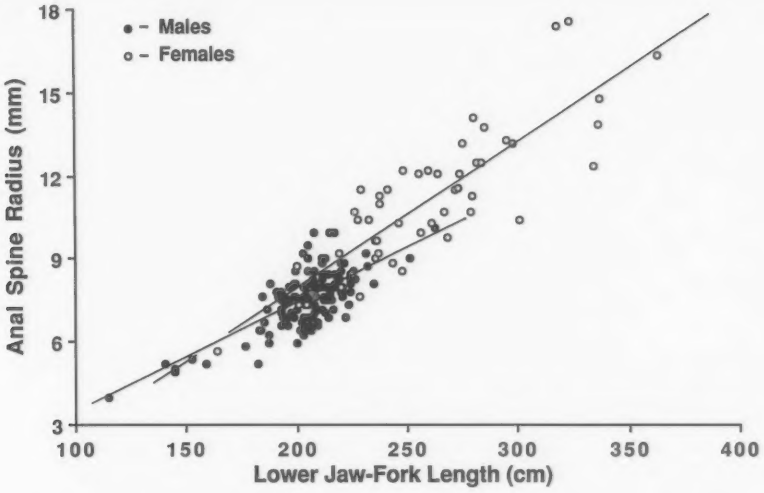


FIGURE 1.—Relationships between lower jaw-fork length (LJFL) and anal spine radius (AR) for male (n = 150) and female (n = 49) Pacific *Makaira nigricans*. Males: AR = −0.5207 + 0.0394 (LJFL) r^2 = 0.52; Females: AR = −2.5879 + 0.0528 (LJFL) r^2 = 0.72.

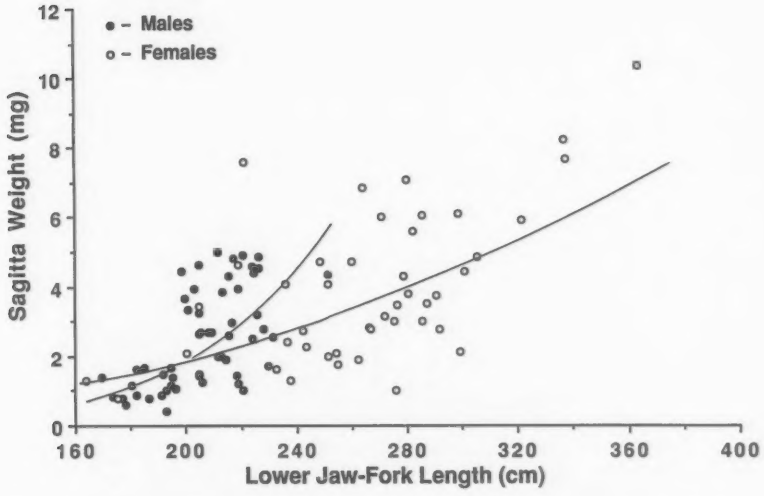


FIGURE 2.—Relationships between lower jaw-fork length (LJFL) and sagitta weight (SW) for male (n = 54) and female (n = 45) Pacific *Makaira nigricans*. Males: SW = 0.0152 * $10^{(0.0103 * \text{LJFL})}$ r^2 = 0.41; Females: SW = 0.3250 * $10^{(0.0038 * \text{LJFL})}$ r^2 = 0.35.

tral areas of the section where the bands were more compressed and clearly delineated. Anal spines were less compressed dorsoventrally than dorsal spines and this may have increased clarity of growth bands (Fig. 3).

Sagittae contained external features that suggested changes in structural growth rate over time. Growth of the rostrum was along two planes. Early growth occurred ventrally to the fish and increments were mainly comprised of

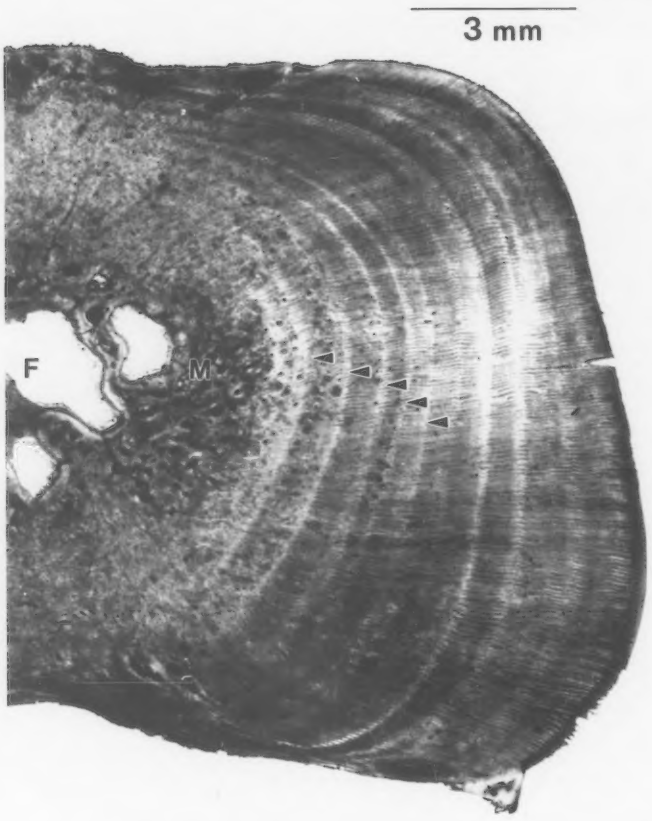


FIGURE 3.—Thin tranverse cross section of the 2nd anal spine from a 138.3 kg female Pacific *Makaira nigricans* as viewed by a binocular dissecting microscope at 63× magnification with transmitted light. Arrows indicate translucent edges of growth bands, F = focus; M = core matrix.

ridges along the anterior rostrum edge (Fig. 5). Between two and four ridges were counted along the anterior edge of the rostrum. Ridges were also visible along the ventral portion of the medial plane of growth (Fig. 6). Most sagittae had an excess of calcium carbonate which hindered ridge quantification to varying degrees (Fig. 6). Several sagittae were difficult to interpret owing to the mottled appearance of the rostrum face.

Vertebrae contained numerous minute (0.05–0.1 mm) concentric growth increments which were topographical features on the centrum face (Fig. 7). There were no prominent 3-dimensional features or changes in ring density which might be indicative of annular events.

Increment Counts and Hardpart Growth

Statistical replacement of early missing anal and dorsal spine bands in larger fish was accomplished by summarizing band radii statistics from smaller fish in which these early increments were visible (Fig. 4). Twenty-one percent of anal spines and 24% of dorsal spines had at least the first and second assumed annulus visible. There was no significant difference ($P <$

FIGURE 5.—Right sagitta from a 35.2 kg female Pacific *Makaira nigricans*. Arrows indicate prominences quantified for estimation of early lateral rostrum growth. R = rostrum; A = antirostrum; C = core region; p = posterior; a = anterior.

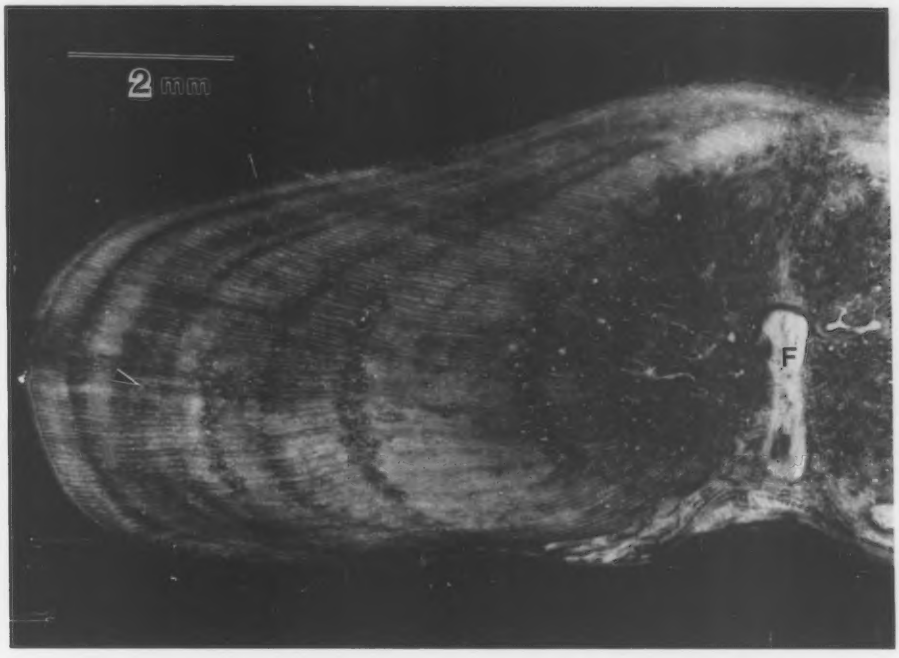
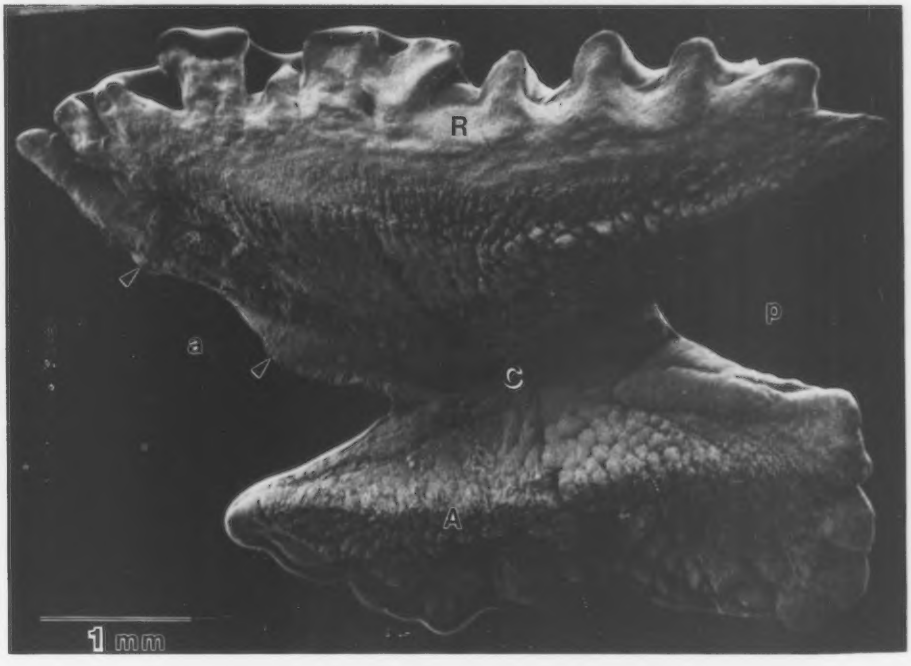


FIGURE 4.—Thin tranverse cross section of the 6th dorsal spine from a 52.4 kg male Pacific *Makaira nigricans* as viewed by a binocular dissecting microscope at 63× magnification with reflected light and a black background. F = focus. Arrow indicates area of multiple rings within a single growth band increment.



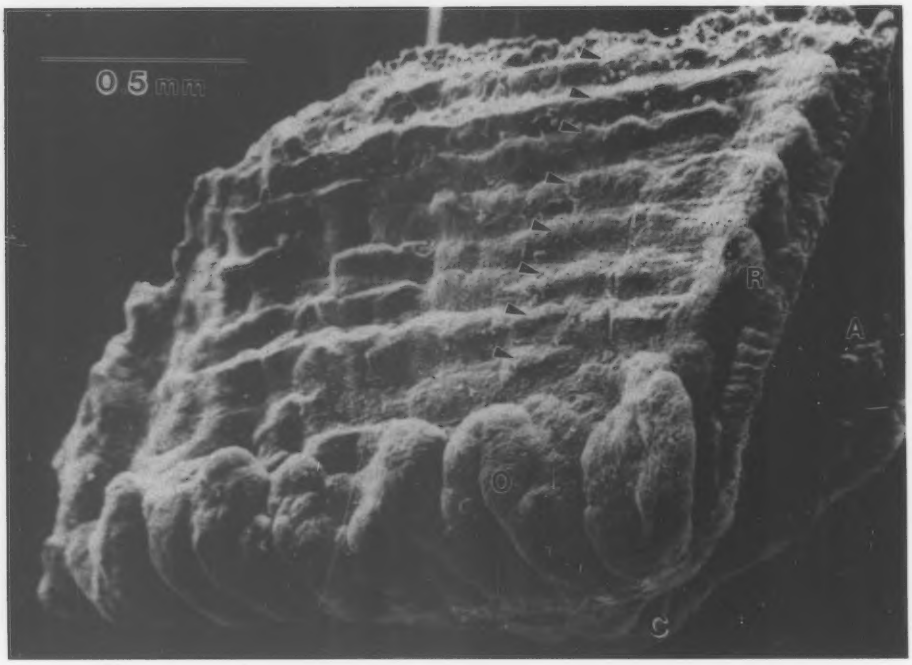


FIGURE 6.—Left sagitta from a 80.1 kg male Pacific *Makaira nigricans*. Arrows indicate rostral ridges quantified for age estimation. R = rostrum; A = antirostrum; C = core region; O = calcium carbonate overburden obscuring ridges.

0.01) between corresponding annuli for these two sets of data for either anal or dorsal spines; therefore, these two data sets were combined. There was, however, a significant difference in corresponding anal and dorsal spine band radii between males and females from the sixth band outward; therefore data were separated by sex (Fig. 8A, B).

Increment counts (sagitta ridges, corrected spine bands, and vertebral increments) increased with hardpart growth for each of the four structures considered. This relationship was logarithmic when increment counts were compared to AR, DR, and SW, and linear when compared to CD for both sexes (Table 3). Coefficients of determination were higher for females in all cases, and ranged from $r^2 = 0.39$ for male dorsal spines to $r^2 = 0.83$ for female dorsal spines.

TABLE 3—Modeled relationships between hardpart growth and increment counts for Pacific *Makaira nigricans*. LJFL = lower jaw-fork length, W = roundweight, AR = anal spine radius, DR = dorsal spine radius, SW = sagitta weight, CD = centrum cone depth, AC = corrected anal spine band counts, DC = corrected dorsal spine band counts, SC = sagittal ridge counts, VC = vertebral increment counts.

Comparison	Equation	r^2 value
Anal fin spines		
Males	$AC = 0.4521 * AR^{1.4316}$	0.62
Females	$AC = 0.5878 * AR^{1.2729}$	0.78
Dorsal fin spines		
Males	$DC = 0.9353 * DR^{1.0044}$	0.39
Females	$DC = 0.5380 * DR^{1.2227}$	0.83
Sagittal otoliths		
Males	$SW = 7.7206 * SW^{0.2941}$	0.41
Females	$SC = 7.1512 * SW^{0.4095}$	0.42
Vertebrae		
Males	$VC = 86.922 + 13.742(CD)$	0.56
Females	$VC = 59.115 + 15.311(CD)$	0.69

Hardpart Comparisons

There was a positive linear relationship between estimated counts of corrected growth in-

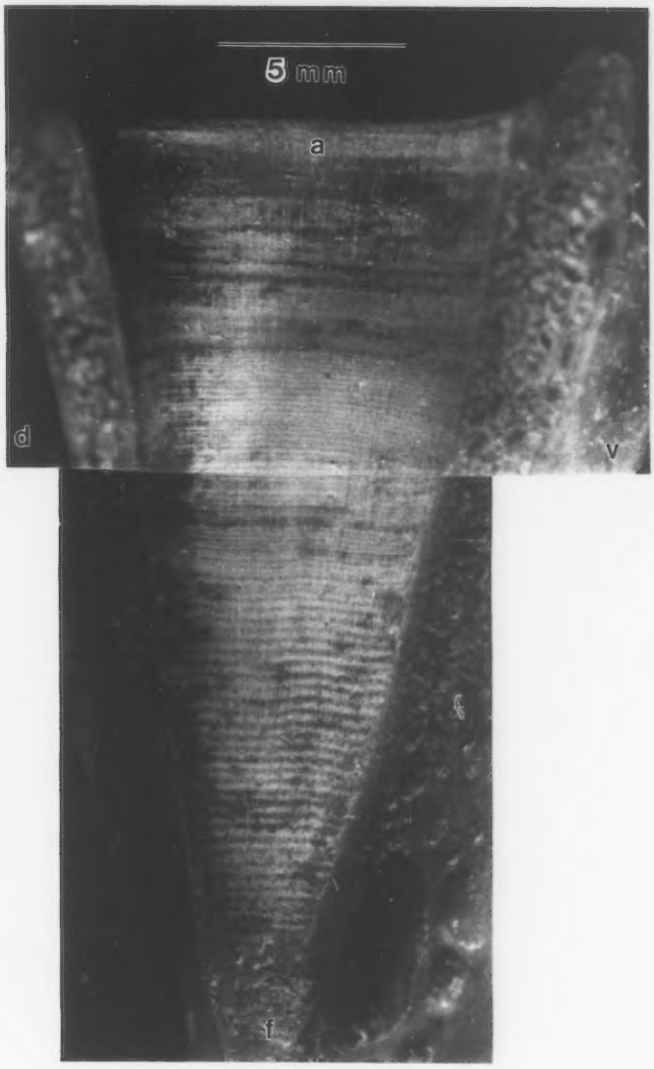


FIGURE 7.—Longitudinal cross section of the anterior centrum from the 23rd vertebrae from a 50.3 kg male Pacific *Makaira nigricans*. a = anterior end; d = dorsal; v = ventral; f = centrum focus.

crements in anal and dorsal spine sections and sagitta from the same blue marlin (Fig. 9A-C). The y-intercepts of these relationships were not significantly different from zero, and the slopes did not differ from parity (slope = 1; $P < 0.05$). Correlation coefficients ranged from $r = 0.84$ ($P < 0.001$) for anal spine and sagitta counts to $r = 0.95$ ($P < 0.001$) for the comparison of anal and dorsal spine counts. The greatest deviation in counts between corresponding hardparts was 9, where the anal spine count was 7 and the sagittal increment count was 16. Wilcoxon Signed Rank tests revealed no statistical difference between counts of these three structures ($P < 0.01$).

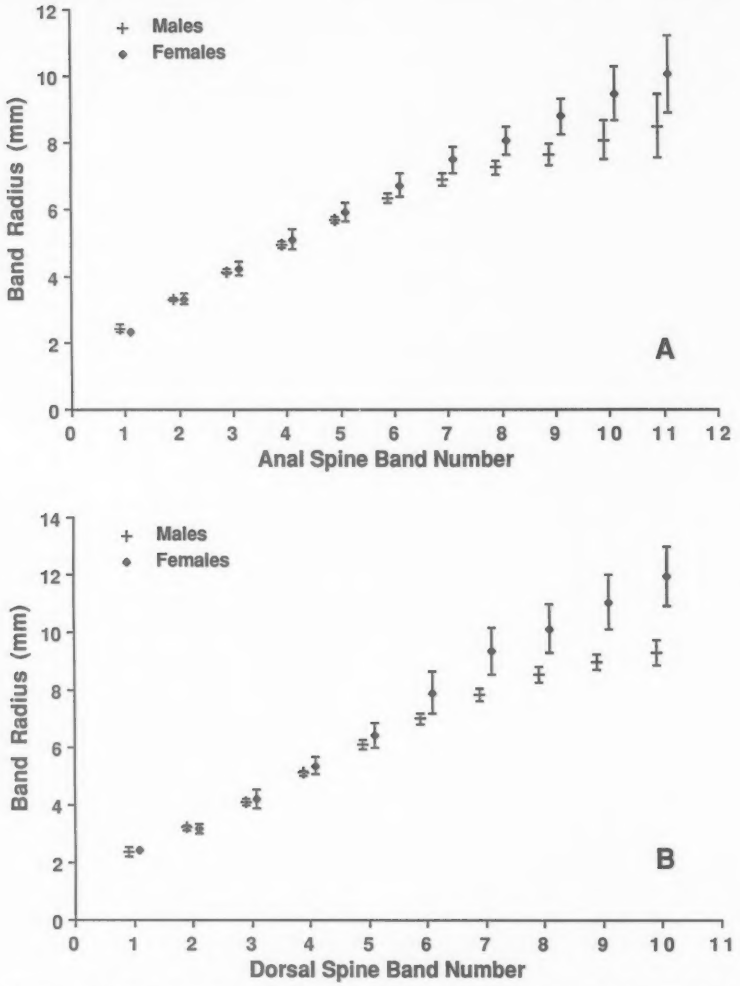


FIGURE 8.—Mean (±95% confidence limits) anal spine (A) and dorsal spine (B) band measurements for male and female Pacific *Makaira nigricans*. Data are from specimens that had at least the first or second band present. All other specimens were assigned inner rings and final age estimates based upon these data.

Reader Comparisons

Average Percent Error (APE) values ranged from 4.88% error for anal spines counted by reader 1 to 9.68% for sagittae counted by reader 2 (Table 4). Reader 1 had lower APE values (more precise age estimations) than reader 2 for each hardpart. Both readers had lowest APE values for anal spines and highest values for sagittae (Table 4).

Comparisons of differences (D) in mean age estimates between readers revealed that reader 1 had a tendency to give higher age estimates

TABLE 4—Average percent error (APE) values calculated from triplicate uncorrected readings of 20 randomly selected anal fin spines, dorsal fin spines, and sagittae.

	Average percent error results	
Hardpart	Reader 1	Reader 2
Anal fin spines	4.88%	8.79%
Dorsal fin spines	5.50%	9.18%
Sagittae	8.15%	9.68%

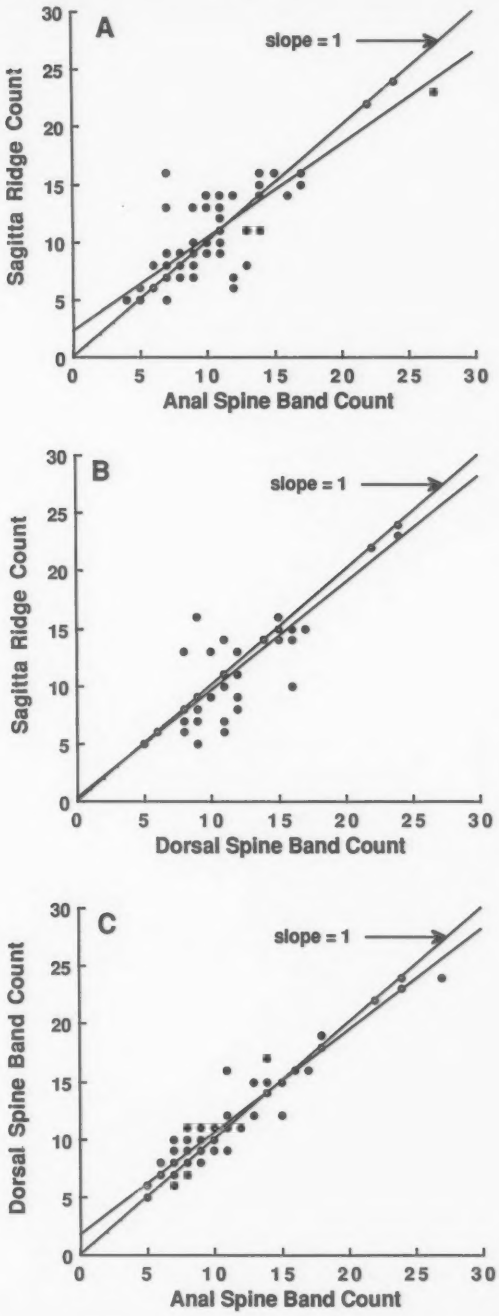


FIGURE 9.—Correlations between coresponding sagittal ridge counts (SC), corrected dorsal spine band counts (DC), and corrected anal spine band counts (AC) for male and female Pacific *Makaira nigricans*. Slopes of the regressions did not differ significantly from parity ($P < 0.05$). SC = 2.2905 + 0.8077(AC) $r = 0.84$; SC = 0.2069 + 0.9300(DC) $r = 0.86$; DC = 1.7682 + 0.8779(AC) $r = 0.95$.

than reader 2 for both anal (D = 0.85) and dorsal (D = 0.55) counts, while reader 2 assigned higher counts to otoliths (D = 1.5) (Fig. 10). None of these count differences differed significantly when compared with a Wilcoxon Signed Ranks test ($P < 0.05$). The greatest difference between mean counts was 8 for otoliths. Overall, there was a greater percentage of age estimates within ±1 and ± 2 years for anal and dorsal spines than for otoliths.

Mean Length at Estimated Age

Based on estimated ages from anal fin spines, there was a pronounced difference in growth between male and female marlin (Fig. 11). Males appear to grow to an average length of 202 cm LJFL at an estimated age of six years, after which growth is determinate. Growth of female marlin, more variable than males, is steady and does not level off as rapidly.

DISCUSSION

Growth patterns observed in dorsal and anal fin spine sections were similar to those described by Jolley (1977) for sailfish, Prince et al. (1984) for Atlantic blue and white marlin, and Wilson (1984) for Pacific blue marlin. Sagittal otolith morphologies were also similar to those from previous studies of Pacific blue marlin (Radtke 1981; Wilson 1984), and rostral ridges were analogous to those validated in one tag-recaptured sailfish specimen (Prince et al. 1986).

Three basic assumptions of the ageing theory are that 1) the growth of a structure used is proportional to growth of the animal, 2) the number of growth increments increase with the growth of the structure, and 3) the observed increments follow a discernible time scale e.g., one year of life (Bagenal 1974). In this study, growth of each hardpart was, to some degree, proportional to growth of the animal's length or weight. Increment counts increased with size of each hardpart, providing further support for the use of these structures for age estimation studies. With the exception of the comparison between SW and LJFL, females had higher coefficients of determination for the relationships between hardpart and somatic growth. This was probably due to the fact that a greater size range of females was sampled. The variable relationship between otolith weight and body size is not surprising since otoliths are so small, relative to

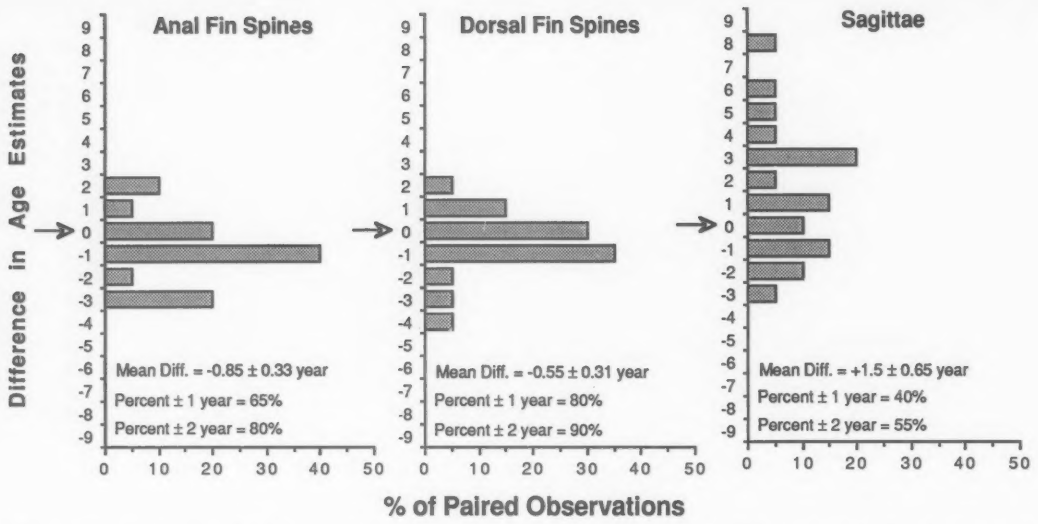

Anal Fin Spines
Dorsal Fin Spines
Sagittae
Difference in Age Estimates
Mean Diff. = -0.85 ± 0.33 year
Percent ± 1 year = 65%
Percent ± 2 year = 80%
Mean Diff. = -0.55 ± 0.31 year
Percent ± 1 year = 80%
Percent ± 2 year = 90%
Mean Diff. = +1.5 ± 0.65 year
Percent ± 1 year = 40%
Percent ± 2 year = 55%
% of Paired Observations

FIGURE 10.—Comparison of differences of mean age estimates between readers (1 minus 2) for anal spines, dorsal spines, and sagittae.

body size. It was expected that fin spines, much larger in size than otoliths, would have a closer relationship to body size. Prince et al. (1984) found a similar relationship between female and male size and hardpart growth for Atlantic blue marlin. The relationship between spine radius and body size may, therefore, be more useful than sagitta weight for back calculation of early growth in marlin. While the first two assumptions of ageing theory have been met, the most important assumption, that increments observed in spines and otoliths of blue marlin represent one calendar year of life, has yet to be proven.

While validation (or, confirmation of the temporal meaning of a growth increment) was not within the scope of this study, partial verification was achieved. Wilson et al. (1983) defined verification as "the confirmation of a numerical interpretation", usually used in reference to the precision of estimated age. Precision was determined by means of comparisons of age estimates from corresponding fin spines and sagittae as well as by means of measurement of error in age estimates within the data and between the data of both readers. In general, there was good agreement in age estimates between sagittae, anal spines, and dorsal spines from the same fish. Prince et al. (1984) described similar relationships between otoliths and dorsal spines of Atlantic blue and white marlin. While the variability of our counts between otoliths and their corresponding spines was greater than between corresponding spines, much of this variation was based on several cases in which the counts of sagittae were as much as 5–10 counts above or below those of corresponding spines. Neither the statistical tests of regression slopes nor the nonparametric tests were able to detect significant deviations from parity; these three structures may deposit increments in relation to similar environmental or growth stimuli.

Comparisons of age estimates, within the data and between the data of both readers provided information on the precision of each technique. Average percent error values of both reader estimates were lower for fin spines than for sagittae, which suggests that fin spine estimates produce a higher degree of precision than sagittae. Similarly, comparisons of differences in mean age estimates between readers revealed greater variability of age estimates resulted from sagittae compared to spines. Variability of sagittal age estimates may be due in part to problems involved with calcium overlayering, and the overlapping, successive ridges, or multiple smaller ridges on these structures. Wilson (1984) reported a similar individual variability in the general morphology and clarity of growth features of Atlantic blue marlin otoliths, and it is reasonable to assume that the interpretation of

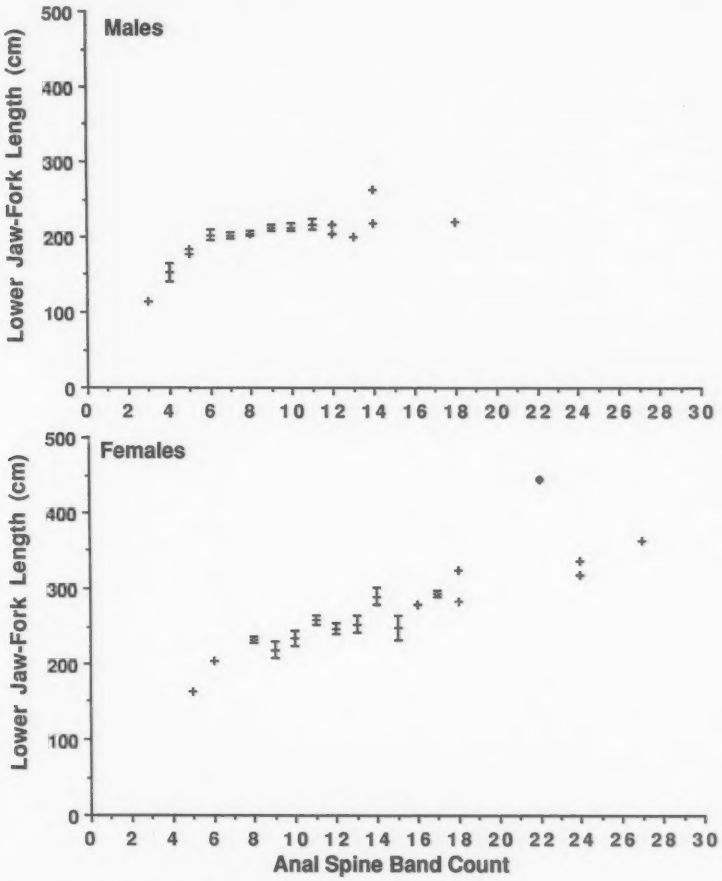


FIGURE 11.—Mean LJFL at age for male and female Pacific *Makaira nigricans* based on anal spine corrected band counts. Vertical lines terminated by narrow horizontal lines represent 95% confidence intervals (male n = 149; female n = 48). Closed diamond indicates estimated age of largest female sampled (748 kg) based upon dorsal spine and sagitta counts.

sagittal growth patterns is more subjective compared with the interpretation of spines.

Based on preliminary age estimates in this study, Pacific blue marlin males have a longevity of at least 18 years and females of at least 27 years of age. The largest female reported in this study was estimated to be 22 years of age based upon both dorsal spine and sagitta counts. The largest male sampled in this study (170.3 kg) was estimatd to be only 14 years of age and the oldest male (estimated age 18) was just above mean size. Wilson's (1984) study of Pacific blue marlin provided similar age estimates and sizes for each sex.

CONCLUSION

1) Anal fin spines, dorsal fin spines, and sagittal otoliths contained growth information which we assumed to be annual in nature and to hold promise for age estimation of this species. Incremental patterns in caudal vertebrae, possibly related to some other environmental or growth stimuli, were not useful for age estimation at this time.

2) Anal and dorsal fin spines are simpler to collect and process than sagittae, and to provide more precise (although not necessarily more accurate) age estimates for this species. The prob-

lem of early growth increment destruction by core matrix expansion can be partially overcome through application of band radius statistics; however, this technique may introduce bias to final age estimates. With the further compilation of band radius statistics and the application of techniques such as discriminate function analysis fin spine counts may also bring final age estimates closer to "true" age.

3) Sagittal otoliths are more difficult to collect and process and have more variable growth rates and morphologies than fin spines. While age estimates based on external features of sagittae are perhaps more subjective, sagittae may provide more detailed information from internal features such as "daily" increments, valuable for age estimation of young of the year.

4) Extensive mark/tag recapture studies are needed to validate the true meaning of the periodicities assumed to be annual.

ACKNOWLEDGMENT

A number of people and organizations made it possible to collect samples for this study, including the fishermen and fishing teams of the billfishing tournaments, the Hawaiian International Billfishing Association, the Pacific Gamefish Research Foundation, Hawaiian Fish Distributors, Jerry Kinney of Volcano Isle Fish Wholesalers, and the Hawaiian Fishing Agency. Bruce Welden, Lisa Natanson, Carol Hopper, and Allison Mallory provided much needed assistance in collecting samples at the tournaments. Eric Masuda, University of Hawaii, assisted in hardpart readings for the APE analyses. Eric Prince and Dennis Lee of NMFS Southeast Fisheries Center, Miami, donated spine samples from the largest female marlin (748 kg) caught in this study and contributed valuable input. This work is a result of research sponsored in part by NOAA, the National Sea Grant College Program, and the Department of Commerce; under grant numbers NA80AA-D-00120 and NA81AA-D-00070, under project numbers R/NP-1-11C, R/F-81, and R/F-84 through the California Sea Grant College Program, under project number PM/M-2ff through the University of Hawaii Sea Grant College Program; and in part by the California State Resources Agency. The David Packard Foundation granted additional travel support.

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Age and Growth of the Blacktip Shark, *Carcharhinus limbatus*, near Tampa Bay, Florida

Kristie A. Killam and Glenn R. Parsons

ABSTRACT: Age and growth of the blacktip shark, *Carcharhinus limbatus*, was investigated in the Tampa Bay area of Florida during May 1985–February 1987. Two hundred and eighteen sharks were captured, and vertebrae were examined from 86 females (52.4–183.0 cm TL) and 54 males (59.8–160.5 cm TL). Minimum and maximum number of translucent winter rings was 0 and 11. Marginal increment analysis on juvenile blacktips with one to three translucent vertebral rings suggested an annual ring deposition during December–January. Length-frequency and length-month analyses suggested three age classes for blacktips <120 cm TL. Growth in length and percentage of size increase of blacktips age 0 and I was 21.0 (29.3%) and 19.0 (20.7%) cm/yr, respectively. Growth in weight and percentage of size increase of age 0 and I blacktips was 3.09 (120.7%) and 3.29 (58.2%) kg/yr, respectively. Age at maturity was 6–7 years (158–162 cm TL) for females and 4–5 years (133–136 cm TL) for males. Maximum age of blacktips captured was 10 years for two females 179.0 and 180.0 cm TL, and 9 years for a 160.5 cm TL male. Growth in weight was fit with a logistic equation. Von Bertalanffy growth parameters for females were estimated at L_∞ = 195.0 cm TL, k = 0.197 and t_0 = −1.154 years and for males, L_∞ = 166.5 cm TL, k = 0.276, and t_0 = −0.884 years.

Blacktip sharks, *Carcharhinus limbatus*, are distributed in all tropical and subtropical continental waters (Compagno 1984) and are very common inhabitants of inshore coastal and estuarine regions in Florida and the Gulf of Mexico (Springer 1940; Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981; Killam 1987). Recently, blacktip sharks have received commercial interest because of their increased value as a food fish. Commercial shark landings in Florida have risen steadily from 170,740 pounds in 1979 to 1,910,222 pounds in 1986 (Florida Department of Natural Resources 1979–86). In California a similar situation has occurred where landings for the common thresher shark, *Alopias vulpinus*, the blue shark, *Prionace glauca*, and the shortfin mako, *Isurus oxyrinchus*, increased from 800,000 pounds in 1976 to 3,500,000 pounds in 1981 (Cailliet and Bedford 1983).

Elasmobranch populations are thought to be easily overexploited because of their relatively slow growth rates, long gestation periods, and low fecundity (Holden 1974, 1977). As apex predators in complex estuarine and marine ecosystems, blacktip sharks have an important ecological role. Increased exploitation of blacktip shark stocks may effect lower trophic levels in the ecosystem, therefore sound life history information is needed. At present, little information is available concerning the biology of the blacktip shark. Its reproductive biology has been examined in the northern (Branstetter 1981) and east-central (Clark and von Schmidt 1965; Killam 1987) Gulf of Mexico. Killam (1987) provided detailed informaton on the seasonal distribution, reproductive biology, and feeding habits of *C. limbatus* captured near Tampa Bay, FL. Dodrill (1977) provided life history information on blacktip sharks captured along the east coast of Florida. Garrick (1982) reported that distinct populations of *C. limbatus* may exist in different geographic regions, because maximum attainable size and sizes at maturity differ markedly between regions.

At present only a single study has been completed concerning the age and growth of the blacktip shark. Branstetter (1987a) estimated growth parameters of *C. limbatus* in the northwestern Gulf of Mexico. This study provides additional information on the age and growth of *C. limbatus* by 1) providing a detailed examination of early growth rates using length-frequency and length-month analyses, 2) utilizing marginal increment analysis on juvenile *C. limbatus* to determine periodicity of ring deposition, and 3) identifying differences in age and growth rates between female and male *C. limbatus*.

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MATERIALS AND METHODS

Two hundred and eighteen blacktip sharks were collected in Tampa Bay and adjacent offshore areas during May 1985–February 1987. One hundred and forty were utilized for age and growth analyses. Sharks were caught with gill nets, longlines, and rod and reel. Once captured, total length (TL), fork length (FL), and precaudal length (PCL) were measured. Total length of embryos was measured with caudal fin extended horizontally. All lengths reported in this paper refer to total lengths. Sharks were then weighed and sexed. Maturity of males and females was determined using morphological and gonadal characteristics described by Clark and von Schmidt (1965) and Wass (1973).

A section of the vertebral column was removed just anterior to the first dorsal fin, although in a few instances only caudal vertebrae were obtainable. The vertebrae were stored frozen, then cleaned of connective tissue by soaking the individual centra in a solution of 5.25% sodium hypochlorite. Centra were then rinsed and stored in a solution of 70% ethanol. Two techniques were tested to determine optimum enhancement of translucent vertebral rings: the silver nitrate technique (Stevens 1975) was compared with a method described by Parsons (1983) in which the vertebral centrum face is shaded with a No. 1 pencil. The latter method detected differences in microtopography of the centrum face and enhanced the translucent rings. This method proved effective and was used because it took only a fraction of the time of the silver nitrate method. Vertebral centra were read under a dissecting microscope at 10× power using transmitted light. Centrum radius was measured from the focus to the dorsal margin using vernier calipers. Radii measurements were used to determine a relationship with shark TL. Ring radii were measured from the focus to each translucent ring, along the angle of the centrum (Fig. 1). Vertebrae collected from the caudal region were excluded from radius and marginal increment measurements. However, caudal vertebrae were utilized in age determinations since ring counts made on centra from different areas of the vertebral column resulted in similar age estimations. Translucent rings enhanced by the pencil method were counted if they extended continuously around the centrum face. Centra were read independently by the two authors. When discrepancies occurred, the vertebrae were reread until an agreement was reached. Ten centra were unreadable and were discarded from the analysis. Twenty centra of varying size were sectioned with a low speed saw through the focus, along the dorsal-ventral plane, for comparative ring counts with whole centra. Since blacktip sharks are born during late April through early June (Killam 1987), ages and growth rates were estimated based on an arbitrary 1 May birth date.

Back-calculated size at age was determined by a direct proportion method (Everhart and Youngs 1981):

$$(TL)_n = (TL)_c \times (VR)_n/(VR)_c$$

where TL_n = calculated length at ring n, TL_c = total length at capture, VR_c = the centrum radius at capture, and VR_n = centrum radius to ring n. Back-calculations were made on blacktip sharks of all sizes.

Marginal increment analysis examines the distance from the most recently deposited ring to the centrum margin and was utilized to determine the time of year that rings are deposited. The centrum margin becomes difficult to resolve in older fish and, therefore, only sharks with one, two, or three rings were utilized in this analysis. Marginal increments were measured from the distal most translucent ring to the edge of the centrum (Fig. 1). Measurements were made with vernier calipers along the angle of the centrum face.

Age and weight relationships were determined by fitting a logistic growth curve to observed data, as described by Kappenman (1981).

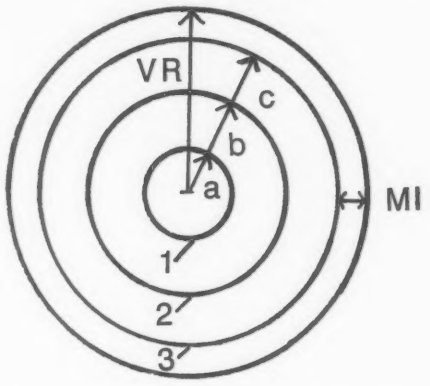

FIGURE 1.—Diagram of typical vertebral centrum of *Carcharhinus limbatus*. Measurements taken include: VR = vertebral radius; MI = marginal increment; a, b, and c = ring radii of translucent rings 1, 2, and 3. Measurements were taken along the dorsal-ventral plane.

The equation is

$$W = a/1 + \exp^{(-(b*r)+c)},$$

where W = weight in kg, a = asymptotic weight in kg, r = number of vertebral rings, and b and c are constants.

The von Bertalanffy (1938) growth equation was used to predict a growth curve for male and female blacktip sharks (Ricker 1975). The equation is

$$L_t = L_\infty(1 - \exp^{-K(t - t_0)}),$$

where L_t = length at age t in years, L_∞ = maximum theoretical length, K = the rate at which the asymptote is reached, and t_0 = the theoretical age at zero length. The von Bertalanffy growth equation was fit to observed data using a nonlinear, Statistical Analysis System method (SAS Institute, Inc. 1982).

RESULTS

Centrum Analysis

A total of 140 vertebral centra were read from 86 female and 54 male *C. limbatus*. These sharks ranged in size from 52.4 to 183.0 cm. The minimum and maximum numbers of translucent rings counted were 0 and 11. Centrum radii ranged from 2.8 to 10.6 mm. Initially, exact agreement of ring counts was reached on 83% of the readings, 15% differed by one ring, and 2% by two rings. Translucent ring counts made on sectioned centra were very similar to those of the corresponding whole centra. The number of translucent rings counted ranged from 1 through 10. When comparisons between whole and sectioned centra were made, exact agreement was reached on 15 centra, 3 centra differed by one ring and 2 centra differed by two rings. In addition, the ring structures counted on the sectioned centra were coincidental with those enhanced by the pencil method. Subjectivity is involved in both methods and sometimes resulted in slightly different counts.

The relationship between blacktip shark total length and centrum radius was linear for both sexes. Analysis of covariance (ANCOVA) indicated no significant difference in the regression lines between sexes, so data were combined into the relationship (Fig. 2)

$$TL = 63.2 + (16.7)R \qquad (r = 0.9797, N = 130)$$

where TL = total length in mm and R = centrum radius in mm.

Initial vertebral ring deposition appeared to occur at or shortly after parturition. Examination of 15 centra from embryonic *C. limbatus*, which ranged in size from 48.4 to 61.8 cm, had no observable translucent ring formation. These sharks were collected between April and June 1986. If a ring had been deposited prior to birth, it should have been visible in the near-term embryos. Free-swimming juveniles captured in late May and early June had a translucent ring deposited on the edge of the centrum. With subsequent growth, this "birth" ring became more apparent as opaque tissue was deposited distally to it.

Marginal increment data on juvenile blacktip sharks (52.4–116.0 cm) of both sexes were combined, because at this age there were no significant differences in sizes (Student's t-test, $P > 0.10$). Fish captured in early February were approximately 9 months old and had very small marginal increments (0.1–0.2 mm), indicating recent ring deposition. Analysis of juveniles taken later in the spring and summer showed that marginal increments increased in width (Fig. 3) to as much as 1.4 mm until December when the next ring formed. This analysis suggests ring deposition occurs during the months of December–January and, in the juvenile blacktip shark, is an annual event.

Early Growth Rates

The relatively large numbers of juvenile and subadult blacktip sharks examined in this study allowed the estimation of early growth rates. A length-frequency distribution of sharks <120 cm TL captured during the months of May–August suggests three separate size classes at approximately 68, 93, and 111 cm (Fig. 4). A length-month distribution (Fig. 5) indicated three distinct size classes for juvenile blacktip sharks <120 cm, and these fish appeared to represent three separate cohorts. Rapid growth of the young sharks produced distinct separations in length and weight between these age classes (Table 1) and each of the sharks examined from these three age classes had one, two, or three translucent rings, respectively. This further supports the annual nature of vertebral ring deposition in juvenile blacktip sharks.

Growth of neonatal sharks was found to be rapid. Mean size of free-swimming juveniles captured during June was 60.5 cm (SD = 3.9, N =

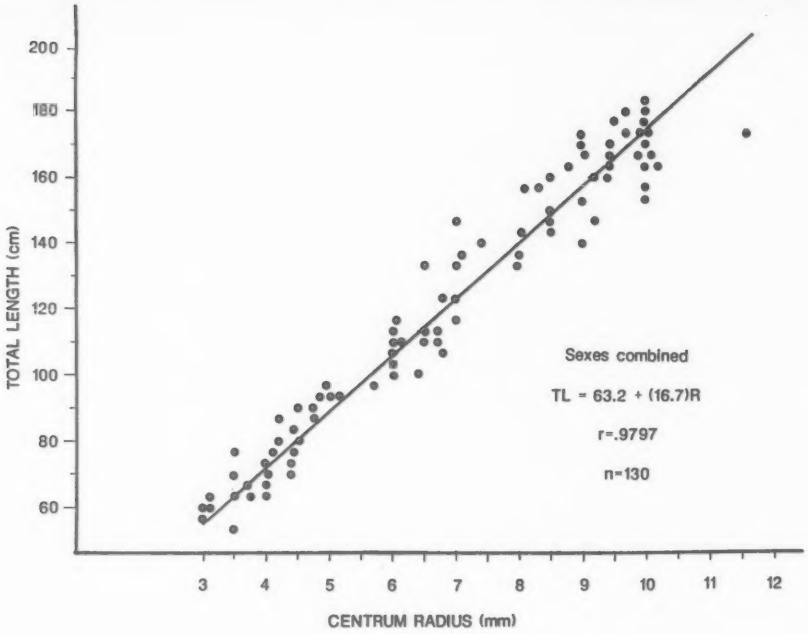

FIGURE 2.—Relationship between vertebral centrum radius and total length (sexes combined) for blacktip sharks captured in the Tampa Bay area of Florida.

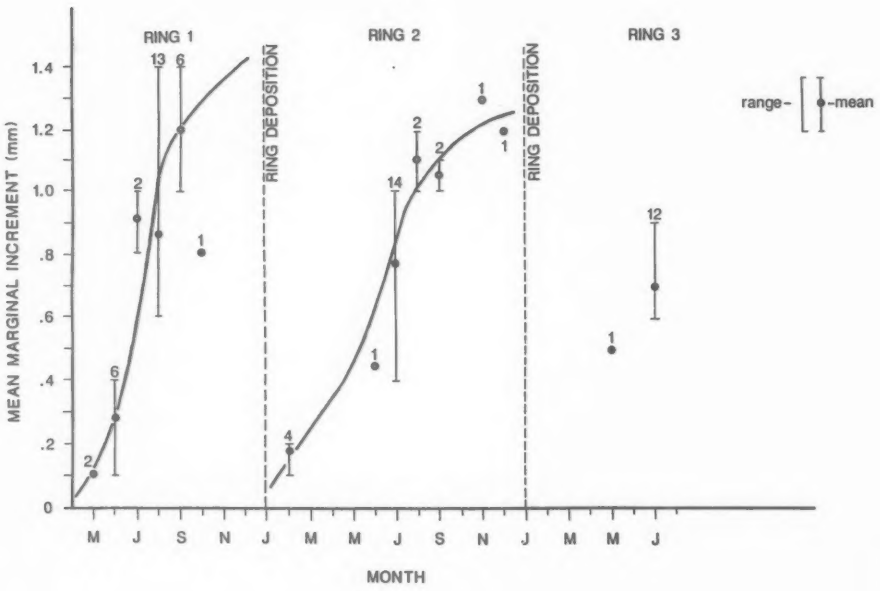

FIGURE 3.—Mean monthly marginal increment correlated with month of capture for blacktip sharks with 1, 2, or 3 vertebral rings. Curves were fit by eye to best approximate the seasonal increase in marginal increment. Translucent ring deposition appears to occur during December or January.

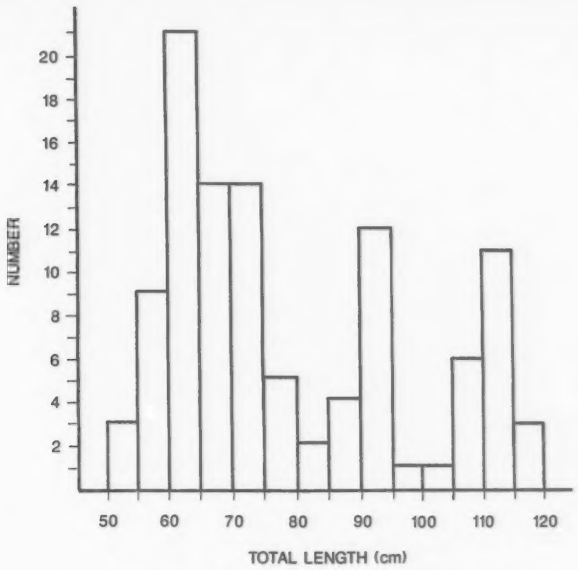

FIGURE 4.—Length-frequency distribution of juvenile blacktip sharks <120 cm TL. Three peaks in abundance are apparent and probably indicative of separate age classes.

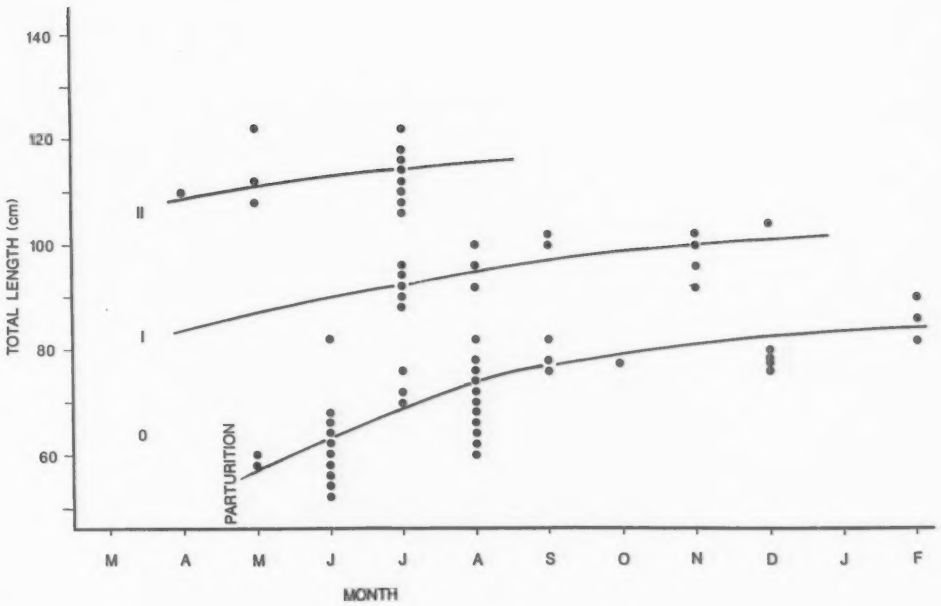

FIGURE 5.—A length-month distribution for juvenile blacktip sharks in age classes 0–II. Curve was fit by eye to best approximate the seasonal increase in total length for each age class.

TABLE 1.—Size differences among juvenile blacktip sharks with 1, 2, or 3 vertebral rings, captured during July and August 1986.

No. rings	No. fish	Mean TL (cm) ± SD	Mean weight (kg) ± SD
1	14	68.7 ± 1.2	2.3 ± 1.2
2	15	93.2 ± 7.3	5.8 ± 1.6
3	15	111.4 ± 8.5	8.9 ± 2.3

33) and mean weight was 1.47 kg (SD = 0.28, N = 29). These fish had prominent umbilical scars which indicated recent parturition. Sharks of this size possessed a birth ring on their vertebral centra and were assigned to age class 0. By mid–August, age 0 sharks had increased 11.1 cm (mean TL = 71.6 cm, SD = 4.74, N = 28), and 1.09 kg (mean weight = 2.56 kg, SD = 0.46, N = 28). This is an increase in length of 18.3% and an increase in weight of 74.0% from mid–June to mid–August. Growth during the first two months was 5.56 cm and 0.55 kg/mo. Four age class 0 *C. limbatus* captured in early February possessed two vertebral rings on their centra and had a mean TL of 85.5 cm (SD = 2.3, N = 4). Compared with the lengths of age 0 fish in mid–August, these fish had grown an additional 13.9 cm or approximately 2.5 cm/mo. This indicates a decline in growth rates over the winter months, and is depicted as a leveling off of the growth curves on the length-month distribution (Fig. 5).

Blacktip sharks captured after May 1 that possessed two vertebral rings (a birth ring and a first winter ring) were assigned to age class I. In late July, these fish had a mean length of 92.6 cm (SD = 2.36, N = 13) and mean weight of 5.65 kg (SD = 0.84, N = 14) representing growth in one year of approximately 21.0 cm (29.3%) and 3.09 kg (120.7%). Age class II sharks (3 vertebral rings) captured in late July had a mean length of 111.8 cm (SD = 3.51, N = 15) and a mean weight of 8.94 kg (SD = 0.80, N = 13) representing an increase of 19.2 cm (20.7%) and 3.29 kg (58.2%) in their second year of growth.

Age-Length

Growth in length was described using the von

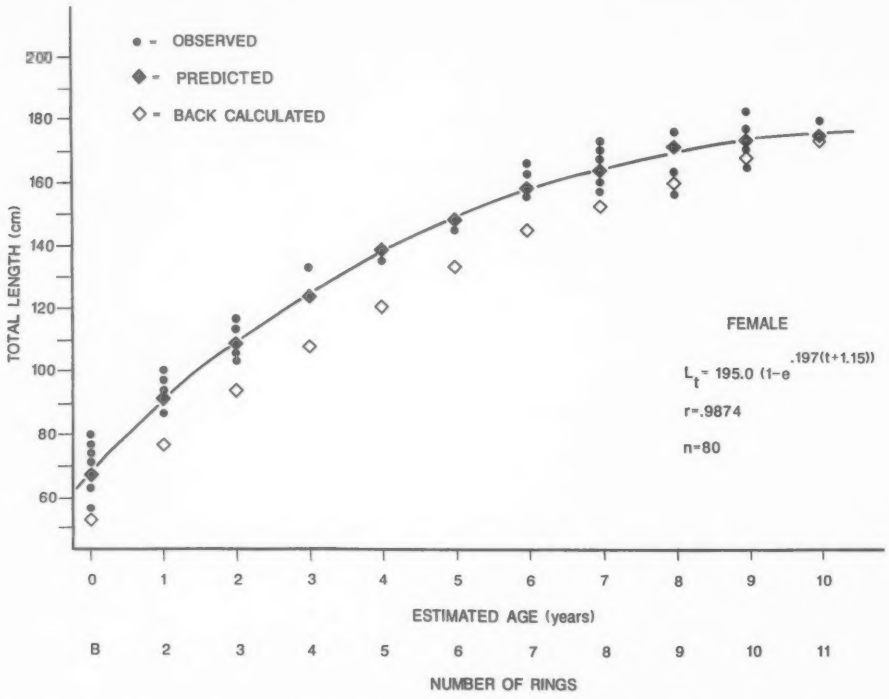

FIGURE 6.—Von Bertalanffy growth curve for female blacktip sharks fit from observed data. Distance between ring B and ring 1 is only 7–8 months but is represented as a 1-yr interval to prevent overestimation of early growth rates.

Bertalanffy growth equation fit with observed data. Growth curves for both sexes were significant at $P < 0.05$. Growth equations produced for female and male *C. limbatus* were

$$\text{Female: } L_t = 195.0\,(1 - \exp^{0.197(t+1.15)})$$
$$r = 0.987,\ N = 80$$

$$\text{Male: } L_t = 166.5\,(1 - \exp^{0.276(t+0.88)})$$
$$r = 0.979,\ N = 53.$$

Estimated maximum total length of females was significantly different from males as indicated by the separation of the calculated 95% confidence intervals. K values, although larger for males, were not significantly different from females (Table 2); however, females were significantly larger than males after age seven (Student's t-test, $P < 0.05$).

Growth rates for juvenile, adolescent, and mature blacktip sharks were approximately 19–21, 9–10, and 3–4 cm/yr, respectively. Females matured at 158–162 cm at 6–7 years; males matured at 133–136 cm at 4–5 years (Killam 1987, Figs. 6, 7). The smallest gravid female captured was six years old. Maximum age obtained by female *C. limbatus* was 10 years for two fish which measured 179.0 and 180.0 cm. Maximum age of male *C. limbatus* was nine years for a fish which measured 160.5 cm.

TABLE 2.—Estimated parameters of the von Bertalanffy growth equation derived using SAS nonlinear method, including 95% confidence intervals.

		Asymptotic 95% confidence interval	
Parameter	Estimate	Lower	Upper
Females			
L_∞(cm)	195.0	183.0	206.9
K	0.1967	0.1546	0.2393
t_0(yr)	−1.154	−1.555	−0.753
Males			
L_∞(cm)	166.5	155.0	177.9
K	0.2758	0.2066	0.3450
t_0(yr)	−0.8836	−1.3006	−0.4665

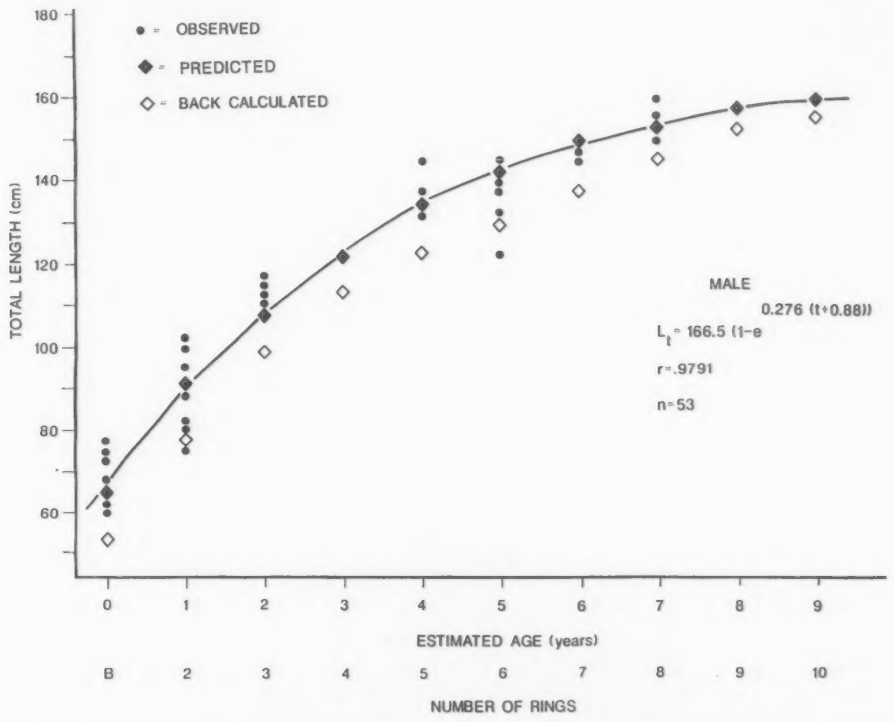

FIGURE 7.—Von Bertalanffy growth curve for male blacktip sharks fit from observed data. Distance between ring B and ring 1 is only 7–8 months but is represented as a 1-yr interval to prevent overestimation of early growth rates.

Back-Calculation

Back-calculated size at time of first ring deposition was 52.1 and 53.2 cm for females and males, respectively. These values correspond closely to observed sizes of *C. limbatus* at birth, further supporting the first translucent ring being a birth ring. Back-calculated size was inspected for "Lee's Phenomenon," which appeared to occur at some ages; however, no consistent trend was identified (Table 3). Mean back-calculated size at age was consistently lower than observed and predicted data (Figs. 6, 7).

Growth curves for both sexes were derived using observed data from sharks with 1–11 vertebral rings. As shown in Figures 6 and 7, ring 1 (birth ring) and ring 2 are shown to be one year apart. In actuality, the second translucent ring is deposited approximately 7–8 months after the formation of the birth ring. However, because 83.4% of these sharks were captured during the summer months of May–September, sharks with two translucent rings are more likely to be at least one year older than those with only the birth ring.

Age-Weight

The nonlinear relationship between shark age and weight was significantly fit with a logistic growth equation ($P < 0.05$). The relationship for females $(W)_f$ and males $(W)_m$ was

$$(W)_f = 42.68/1 + \exp^{-(0.540*r)-3.14}$$
$$r = 0.962, N = 69$$

$$(W)_m = 27.83/1 + \exp^{-(0.550*r)-2.58}$$
$$r = 0.974, N = 48$$

where W = weight in kg, and r = number of translucent rings (Figs. 8, 9). Growth in length and weight of *C. limbatus* appears to reach an asymptote, and blacktips greater than 10 years old probably grow very little each year.

TABLE 3.—Mean back-calculated total lengths (cm) at age, for female and male blacktip sharks captured in the Tampa Bay area of Florida.

Rings	Number	Mean	±	SE	B	1	2	3	4	5	6	7	8	9	10
Females															
B	19	68.1	±	8.0	54.3										
2	16	88.7	±	7.5	54.6	79.6									
3	5	109.7	±	4.1	49.2	77.6	101.0								
4	1	132.0	±		57.2	88.0	114.4	125.9							
5	1	136.4	±		49.9	68.2	96.5	113.1	126.4						
6	2	142.0	±	7.2	51.5	70.2	87.9	104.8	119.8	133.0					
7	2	157.0	±	10.1	50.9	69.9	88.0	103.6	119.2	133.9	144.2				
8	12	165.8	±	6.2	48.7	72.6	96.1	111.9	126.9	138.2	149.9	159.5			
9	6	166.4	±	8.0	48.5	66.8	85.4	100.7	114.1	127.0	137.9	138.8	158.6		
10	3	172.3	±	4.9	48.9	68.7	86.9	102.2	116.0	128.6	139.1	150.6	162.7	168.8	
11	2	179.1	±	7.6	51.0	69.9	87.9	103.1	119.3	131.0	140.8	149.8	157.9	170.3	176.5
Weighted mean					52.0	74.3	93.2	107.4	121.4	133.5	144.5	154.7	159.6	169.4	176.5
Number of back-calculations					69	50	34	29	28	27	25	23	11	5	2
Growth increment					22.6	18.9	14.2	14.0	12.1	11.0	10.2	4.9	9.8	7.1	
Males															
B	16	68.0	±	6.9	55.5										
2	12	89.4	±	8.7	53.0	79.7									
3	9	112.3	±	3.5	50.5	76.9	101.1								
4	1	122.0	±		56.1	79.4	103.6	125.6							
5	3	138.3	±	5.4	52.9	75.8	97.3	117.3	130.4						
6	3	135.7	±	8.8	51.1	75.5	95.3	109.0	120.3	132.8					
7	2	145.8	±	10.6	53.7	76.7	96.6	111.2	119.5	128.7	140.2				
8	1	155.1	±	5.4	51.7	72.4	93.1	110.3	120.7	132.8	141.4	148.3			
9	2	155.8	±	3.9	52.2	75.7	89.6	103.6	118.4	127.1	137.5	144.4	151.4		
10	1	160.5	±		46.7	63.8	95.0	110.6	118.4	126.2	134.0	140.0	148.0	154.3	
Weighted mean					53.2	77.2	97.8	112.0	122.3	129.9	138.4	144.2	150.3	154.3	
Number of back-calculations					50	34	22	13	12	9	6	4	3	1	
Growth increment					24.0	20.6	14.2	9.4	7.6	8.5	5.8	6.1	4.5		

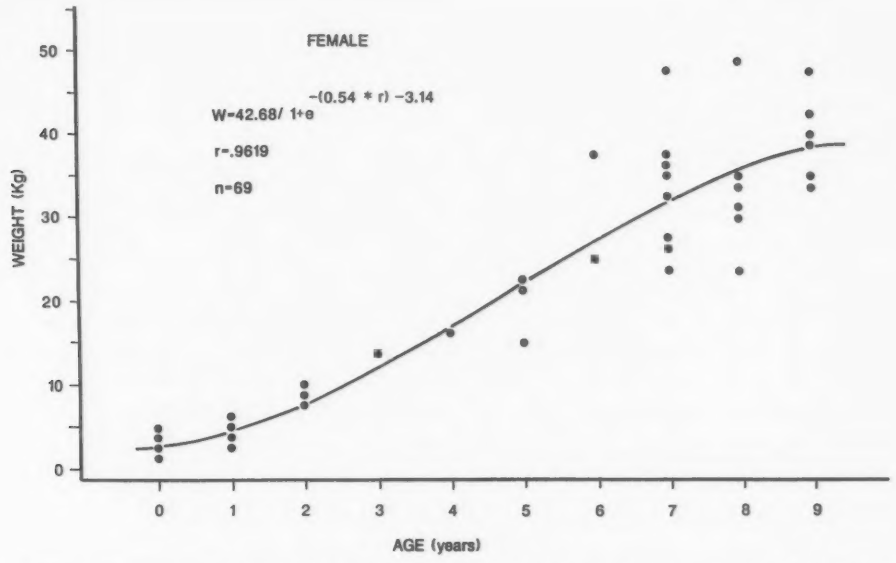

FIGURE 8.—Age-weight relationship for female blacktip sharks; logistic growth equation provided a significant fit to the data ($P < 0.05$).

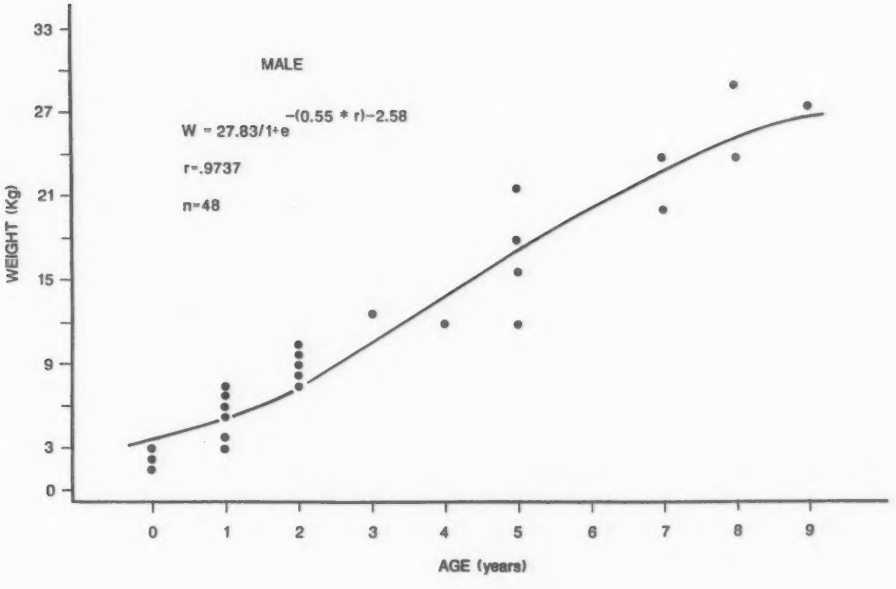

FIGURE 9.—Age-weight relationship for male blacktip sharks; logistic growth equation provided a significant fit to the data ($P < 0.05$).

DISCUSSION

Centrum analysis

Perhaps the most common limiting factor in many studies concerning shark species is the acquisition of sufficient specimens over the entire size range of the species. The relatively large sample size reported here made annulus verification and subsequent growth estimation possible. Marginal increment, length-frequency, and length-month analysis suggest that ring periodicity in juvenile *C. limbatus* is annual. Annual ring deposition in sharks has been verified or validated for several species, including *Prionace glauca* (Stevens 1975), *Rhizoprionodon terraenovae* (Parsons 1983), *Negaprion brevirostris* (Gruber and Stout 1983), *C. amblyrhynchos* (Radtke and Cailliet 1984), *Triakis semifasciata* (Smith 1984), *C. plumbeus* (Casey et al. 1985), *C. leucas* (Branstetter and Stiles 1987), *C. falciformis* and *Sphyrna lewini* (Branstetter 1987b), *Galeocerdo cuvieri* Branstetter et al. 1987), and *S. tiburo* (Parsons 1987). Cailliet et al. (1986) provided an extensive review of elasmobranch species for which age and growth rates have been estimated. In some lamnoid species such as *I. oxyrinchus* (Pratt and Casey 1983) and *Cetorhinus maximus* (Parker and Stott 1965), deposition of two rings per year has been suggested. Therefore, it appears that for each species being examined, periodicity of ring deposition must be verified or validated before proper age and growth estimates can be attained.

Early Growth

Because Tampa Bay is a nursery area for *Carcharhinus limbatus* (Killam 1987) the capture of numerous juvenile specimens was fairly easy. Rapid early growth rates of these young sharks made determination of periodicity of ring deposition possible. Marginal increment analysis suggested that one translucent ring is deposited during the winter months of December–January, and that opaque tissue is deposited distally to these rings, during periods of rapid growth in warmer months. A similar pattern of ring deposition has been identified in *C. amblyrhynchos* (Radtke and Cailliet 1984; Cailliet et al. 1986). The opaque areas have been found to contain higher amounts of calcium and phosphorus than the adjacent translucent rings.

The rapid early growth of juvenile *C. limbatus* produced distinct separations in length-frequency modes for sharks <120 cm TL. Modes are more difficult to resolve in larger *C. limbatus* because fish of similar sizes may represent a variety of age classes owing to differences in individual growth rates and the decrease in growth rate as age increases. Ketchen (1975) utilized length-frequency analysis to estimate early age classes of *Squalus acanthias*, 44–70 cm TL. It appears that only early age classes of sharks undergoing rapid growth can be estimated by analyzing length-frequency distributions. Casey et al. (1985) found that in 3–8 year old *C. plumbeus*, several age classes may be represented at any one length.

A length-month distribution subjectively assigned *C. limbatus* to age classes and provided estimates of growth rates. Modes identified by this method were subjectively assigned to age classes. Three age classes were apparent for blacktips 62–118 cm. As with the length-frequency distributions, the length-month distribution becomes increasingly difficult to resolve in older sharks. Pratt and Casey (1983) utilized this method to estimate three age classes of juvenile *I. oxyrinchus*, 54–175 cm TL. Parsons (1985) used this procedure to estimate age and growth through maturity for the rapidly growing *R. terraenovae* whose males mature as early as 2.0–2.4 years and females mature at 2.4–2.8 years.

Early growth rates have been examined in only a few species of sharks. Juvenile *C. leucas* grew at 18 and 16 cm/yr during the first 2 years, respectively, decreasing to 11 cm/yr in larger sharks (Thorson and Lacy 1982). *Rhizoprionodon terraenovae* growth rates for age classes 0 and I were 30 and 10 cm, respectively, which corresponded to a 100% increase in length for age 0 individuals and a 15% increase at age I (Parsons 1983). Young *N. brevirostris* growth rates did not exceed 25 cm/yr and probably averaged 10–20 cm/yr (Gruber and Stout 1983). *Galeocerdo cuvieri* appeared to grow > 20 cm/yr until near maturity (Branstetter et al. 1987). *Carcharhinus limbatus* had growth rates of 21.0 and 19.2 cm/yr for age classes 0 and I. A very similar growth rate was determined for juvenile *C. limbatus* in the northern Gulf of Mexico (Branstetter 1987a).

It appears that early growth in more pelagic species may differ. Young *I. oxyrinchus* showed rapid first year growth rates of 49.0 cm/yr and second year rates of 32.0 cm/yr (Pratt and Casey 1983). They found that growth of *I. oxyrinchus*

was more similar to other species of pelagic fish such as the blue shark, dolphin, and tuna.

Age-Weight

While growth in length was fit with the von Bertalanffy growth equation, a logistic equation provided a significant fit to age-weight data. In a similar manner, Parsons (1987) reported that *Sphyrna tiburo* age-weight data were best fit with a logistic equation. Both the von Bertalanffy and logistic growth equation imply that the increase in length and weight of *C. limbatus* is asymptotic. Ricker (1979) cited contrasting opinions on the feasibility of asymptotic growth for fishes, and stated that usually a few older individuals in a fish population may be considerably larger than the asymptote, particularly in terms of weight. *Carcharhinus limbatus* >10 years old probably grow very little in length each year. The results of this study suggest that *C. limbatus* tends toward a W_∞, and appear to grow very little in weight at older ages.

Age and Growth Estimates

The von Bertalanffy growth equation closely described the growth of *C. limbatus*. Estimated size at birth was approximately 53.0 cm which corresponds closely to that of observed data. Maximum theoretical length from the von Bertalanffy growth equation was 195.0 cm for females and 166.5 cm for males, similar to the maximum length of females and males collected during this study, 183.3 and 165.0 cm, respectively. Maximum lengths reported for *C. limbatus* in the Gulf of Mexico were 191.0 and 175.0 cm for females and males, respectively (Clark and von Schmidt 1965); within the 95% confidence intervals predicted for L_∞ (Table 2). Branstetter (1987) estimated L_∞ at 176.0 cm for blacktip sharks captured in the northwestern Gulf of Mexico although his estimates were with sexes combined (34 females, 13 males). Because growth curves differ between males and females, this underestimates L_∞ for females and overestimates L_∞ for males. This may also influence estimated ages of maturity for the sexes; for example, males included in the growth curve would slow the rate at which the curve approaches a particular size and thus result in an older estimated age at maturity for females.

A positive linear relationship between shark length and centrum radius has been established in many shark species. In *I. oxyrinchus* (Pratt and Casey 1983) and *G. cuvieri* (Branstetter et al. 1987), a curvilinear relationship may be more applicable to the data. In either situation, this allows back-calculation of length at time of ring deposition. Back-calculated sizes were smaller at each age class than sizes from observed and predicted data (Table 3, Figs. 6, 7). Ring deposition occurs during the winter months of December–January; however, 83.4% of the blacktips were captured during May–September; thus the increase in size between time of ring deposition and time of capture produced the above disparity. This situation is less evident in older *C. limbatus* with decreased annual growth rates.

Growth rates estimated for adolescent and mature *C. limbatus* were 9–10 and 3–4 cm TL/yr, respectively. These rates were similar to those found by Branstetter (1987a) in the northwestern Gulf of Mexico, although he reported that lengths at age for female and male *C. limbatus* were similar. This study found a significantly larger total length of females at age 7 or greater. Age at maturity for blacktips captured in the Tampa Bay area and in the northwestern Gulf of Mexico were similar for males (4–5 years) but differed among females. Females reach maturity in 6–7 years near Tampa Bay, and 7–8 years in the northwest Gulf of Mexico. Similarity of life history parameters for *C. limbatus* captured in the Tampa Bay area (Killam 1987), in the east central Gulf of Mexico (Springer 1940; Clark and von Schmidt 1965), and in the northern Gulf (Branstetter 1981, 1987a) suggest a continuous population of this species in the Gulf of Mexico.

ACKNOWLEDGMENTS

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Effects of Nonrandomness on Line Transect Estimates of Dolphin School Abundance

Elizabeth F. Edwards and Pierre M. Kleiber

ABSTRACT: Line transect analysis is a census method that has been used to derive estimates of dolphin school abundance from sightings data collected by observers on tuna purse seine vessels. The method is based on the assumption that movements of the sighting platform (tuna vessel) and sighted objects (dolphin schools) are random with respect to each other. In practice, neither schools nor vessels move randomly. Stratification of sightings data has been used to alleviate partially the effects of this nonrandomness, but the effectiveness of this stratification cannot be tested with data from commercial vessels because the movements of the vessels cannot be controlled.

As an alternative, we have used a relatively simple mathematical simulation model to investigate the severity of bias introduced into school abundance estimates by nonrandom movements of schools and vessels, and by the data stratification procedure. Simulations show that nonrandom movements on a scale of a few hundred miles, coupled with the data stratification procedure, can lead to overestimates of dolphin school abundance by as much as a factor of two. These results focus attention on the need to understand patterns of dolphin school distribution in smaller scales of space and time than have been studied previously, and to develop data stratification methods more robust against the effects of small-scale nonrandomness.

The National Marine Fisheries Service (NMFS) monitors mortality of dolphins involved in fishing operations by the United States purse seine fleet for yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific Ocean (ETP), to determine whether mortality has exceeded an annual quota implemented by an act of the U.S. Congress. The quota levels depend upon whether dolphin populations are thought to be increasing or decreasing in number, relative to population levels during previous years.

The most effective method currently available for detecting trends in relative abundance is analysis of population abundance estimates collected over a period of 5–15 years. The most effective method currently available for making these abundance estimates is line transect analysis of dolphin school sightings data (Holt 1987; Buckland and Anganuzzi 1988). Two data sources are available for these line transect estimates of abundance: 1) data collected by observers during research surveys (RSOD—Research Survey Observer Data) and 2) data collected by observers during commercial fishing operations (TVOD—Tuna Vessel Observer Data). NMFS has used RSOD because research surveys can be designed specifically to satisfy the assumptions required by line transect analysis (Smith[1]). However, research surveys are very expensive and are becoming more so. This expense causes RSOD to be sparse relative to TVOD and possibly unavailable in the future.

TVOD are a potential solution to these problems, having three significant advantages over RSOD: TVOD are much more abundant, are relatively inexpensive, and are likely to continue being collected as long as fishermen set on and kill dolphins. Observer-days from tuna vessels account for roughly 95% of the annual observer effort in the ETP, while observer-days from research vessels account for only 5%. TVOD are inexpensive relative to RSOD because TVOD are collected by the observers in addition to monitoring dolphin mortality, the latter being the main reason the observer program was initiated. This monitoring program has been in operation for the past 14 years, will continue into the foreseeable future, and monitors about 30% of trips by purse seiners (both U.S. and non-U.S. vessels) each year in the ETP[2]. Ideally, TVOD could be used in place of RSOD to monitor changes in abundance of dolphins.

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Fishery Bulletin, U.S. 87: 859–876.

[1]Smith, T. D. 1975. Estimates of sizes of two populations of porpoise (*Stenella*) in the eastern tropical Pacific Ocean. Admin. Rep. No. LJ-75-67. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[2]Inter-American Tropical Tuna Commission, Annual Reports 1980–1988. Scripps Institution of Oceanography, La Jolla, CA 92038.

Reluctance to use TVOD to monitor the relative abundance of dolphins stem from concerns that TVOD 1) seriously violate some of the fundamental assumptions of line transect analysis (Polachek 1983), 2) are subject to serious but unquantified and possibly inconsistent biases, and 3) may be plagued with artifacts arising from the data collection process. Artifacts include, for example, differences between RSOD and TVOD in the sighting frequencies of various dolphin species reported by observers on research vessels compared to tuna vessels (Barlow and Holt[3]), environmental factors affecting sighting ability (e.g., sun glare, sea state, and cloud cover; Holt and Cologne 1987), and shifting areas of concentrated search effort (Buckland and Anganuzzi 1988). However, problems of this type are common to most commercial fisheries data and analyses derived from them. It is important to determine whether, despite these difficulties, useful estimates can be derived from such data sets.

Toward this end, we have developed a relatively simple model simulating the TVOD collection process. Our purpose in developing the model was twofold: 1) to test the effect of suspected biasing factors on line transect estimates of abundance and 2) to test new methods of abundance estimation prior to conducting expensive field tests. There are two unique advantages of simulation modeling in this context. First, we are simulating dolphin abundances and vessel movements within the model itself; therefore, we have available the "truth" against which to compare our model-generated estimates of abundance. Second, we have the capability of investigating effects on estimates that are due to combinations of biasing factors which may not have occurred during the years we happen to have been collecting data, but which can be expected to occur. Biasing factors include, for example, small-scale nonrandomness in school and vessel movements and spatial distributions, choice of data stratification method, changes in fishing objectives, practices, and areas of concentrated search, and changes in sighting protocol and recording procedures. We chose to focus first on the effects of nonrandomness and on the method of data stratification because recently developed methods of line transect analysis to estimate dolphin abundance from TVOD (Buckland and Anganuzzi 1988) raised serious but unanswered questions about the effects of these factors on the abundance estimates derived.

The philosophy behind building a relatively simple model was that biases shown to be troublesome and methods shown to be inadequate in a simple computer model are likely to be even more troublesome and inadequate in the real world. It is both more efficient and more economical to investigate these biases and methods first with a simple simulation model, prior to developing expensive field experiments. We have specifically applied the tenets of Occam's Razor in developing this model, making it as simple as possible while still incorporating the major processes and features contributing to the TVOD data collection process. In this study, we focused only on estimating abundance of dolphin *schools*, leaving questions about abundance of *individual* dolphins for a later day. We also assumed that data were collected without artifacts, leaving also that problem for a later set of simulations. Both of these omissions are examples of factors that probably have strong effects on analyses of TVOD, but which are at this stage unnecessary refinements to the simulation model. Such refinements could be added later if no problems were identified during simulations with the early, most simplified versions of the model.

This paper presents results of testing one hypothesis about one of the most fundamental factors suspected to affect seriously line transect estimates of dolphin abundance derived from TVOD. Specifically, we tested the effect of nonrandom clustering by dolphin schools on abundance estimates. As part of this analysis we tested also the effects of three types of data stratification prior to line transect estimation of school abundance: 1) no stratification, 2) stratification by raw encounter rate per 1° square, and 3) stratification by smoothed encounter rate per 1° square, using the smoothing and interpolation algorithm developed by the Inter-American Tropical Tuna Commission for deriving estimates of dolphin abundance from line transect analysis of TVOD (Buckland and Anganuzzi 1988). We were primarily interested in the third type of stratification, because the properties of the smoothing algorithm are poorly understood. The other two stratifications were conducted to provide a basis for comparison with the smoothing procedure.

[3]Barlow, J., and R. S. Holt. 1986. Geographic distributions of species proportions for dolphins in the eastern tropical Pacific. Admin. Rep. No. LJ-84-27. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

THE MODEL

Model Structure

This section presents a general description of model structure. A detailed technical explanation of the model can be found in Kleiber and Edwards[4]. The model (TOPS: Tuna-vessel Observer Program Simulator) simulates the movements of 75 tuna purse seiners and either 2,500 or 1,250 dolphin schools within a 1,200 × 1,200 square nautical mile area. Figure 1 provides a graphical comparison of the "study area" simulated by the model, to the entire area within which the tuna-dolphin association is exploited by the purse seine fleet. Twenty-five hundred dolphin schools is the nominal number of schools expected within a 1,200 × 1,200 nmi area of the ETP, based on Holt's (1985,[5,6] 1987) estimates of the total number of dolphins, average size of dolphin schools, and species proportions for the ETP, prorated from the entire ETP to an area 1,200 × 1,200 nmi. Simulations were also run with half this number of schools to investigate the ability of abundance estimates derived under different conditions to reflect changes in actual abundance in the model. Number of vessels is based on reported size of the ETP purse seine fleet, assuming about 50% of the fleet will be fishing a given area of this size at any one time (see IATTC Annual Reports 1983–87).

All dolphin schools are assumed to be identical (i.e., are replicates); all schools include only the

[4]Kleiber, P. K., and E. F. Edwards. 1988. A model of tuna vessel and dolphin school movement in the eastern tropical Pacific Ocean: technical description of the model. Admin. Rep. No. LJ-88-28. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[5]Holt, R. S. 1985. Estimates of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin fishery. Admin. Rep. No. LJ-85-16. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[6]Holt, R. S. 1985. Estimates of population size of dolphins in the eastern tropical Pacific using line transect methods. Admin. Rep. No. LJ-85-20. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

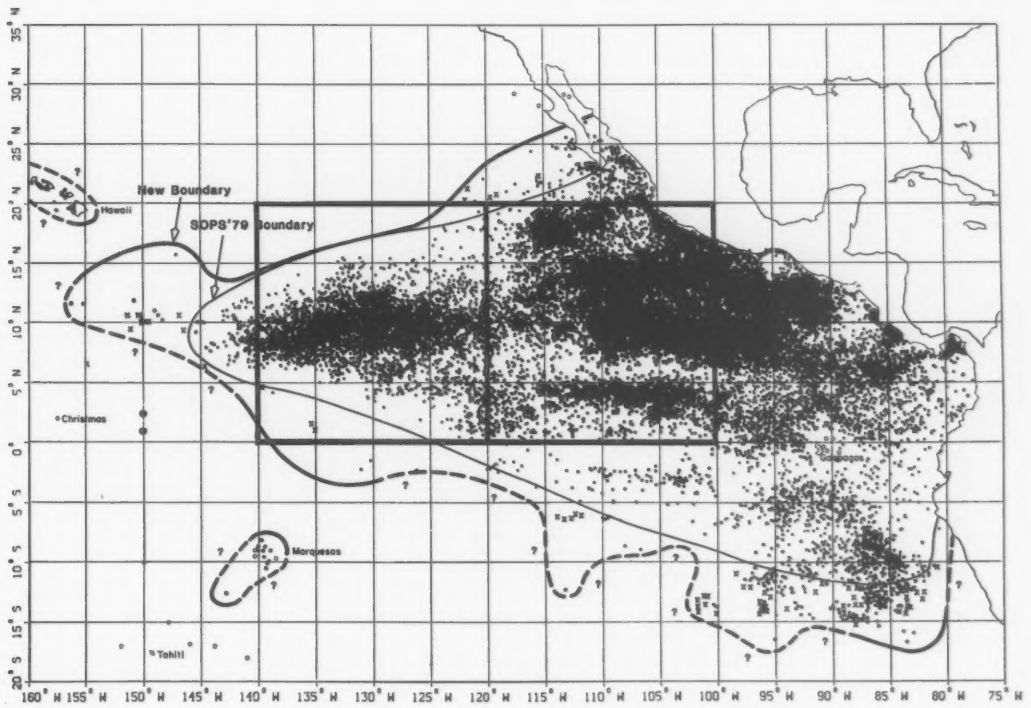


FIGURE 1.—Approximate extent of the eastern tropical Pacific Ocean (ETP) tuna purse seine fishery. Boxes enclose two areas the size of the area simulated by TOPS (1,200 × 1,200 nmi), indicating relative sizes of the entire fishery area compared to the area encompassed by the simulation.

northern offshore stock of spotted dolphins, *Stenella attenuata*, all have the same number of animals, all are equally visible, and all move independently of each other. All vessels are assumed to be identical also; they are the same size, are equally adept at sighting dolphin schools, and do not communicate with each other. Dolphin schools move at speeds varying between 0.5 and 2.4 knots, depending on conditions of the local environment (see below). All vessels move at 15 knots continuously. Speeds are based on reported averages for dolphin schools (Perrin 1979) and for vessels (vessel activity records, NMFS data bases). Vessels are assumed to chase and set upon all sighted schools. Vessels that have set on a school are "removed" from the simulation for 5 hours, simulating the average time to chase, set, collect tuna, release dolphins, and get back under way. Sighted schools are removed from the position of sighting and replaced randomly within 0 to 50 nmi of the sighting, simulating a variable "rest" period of 0 to 24 hours between one set and the next for sighted schools.

Dolphin schools move in response to the local height and gradient of an "environmental topography". The topography is a grid of equally spaced peaks of good habitat interrupted by valleys of low-quality habitat. Habitat quality varies between a value of 1 at the peaks for optimum habitats to 0 at the least favorable habitats midway between peaks. Topographies are generated as a function of sine waves in two-dimensional space and are either stationary or made to slide from right to left at 1 knot. Two combinations of peak spacing and peak shape were used for the simulations reported here: 1) a simple topography of 4 equally spaced peaks with relatively gentle slopes (Fig. 2a), and 2) a more complex topography of 16 equally spaced peaks with relatively steep slopes (Fig. 2b).

These choices for peak number generate spaces between peak tops of 300 and 600 miles. These spacings were chosen based on approximate distances between clusters of dolphin school sightings from research vessel data[7]. Peak steepness was chosen to simulate either slow spatial changes in environmental conditions (gentle slope) or rapidly changing conditions (steep slope) such as those which pertain at ocean fronts (Owen 1981).

Spacings of 600 miles between gently sloping peaks generates distances of 300 miles between maximum and minimum values of the environ-

[7]R. S. Holt, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. July 1987.

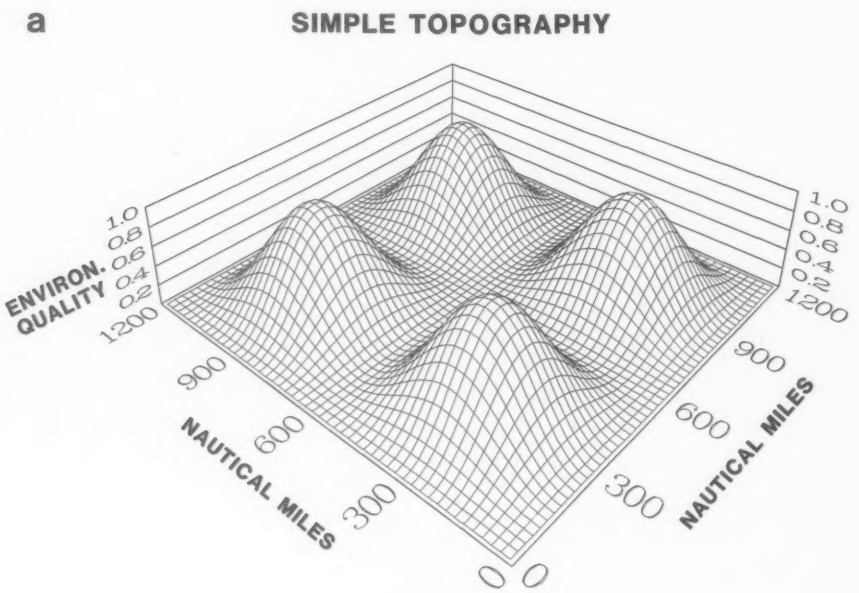


FIGURE 2.—Geometric configuration of the simple environmental

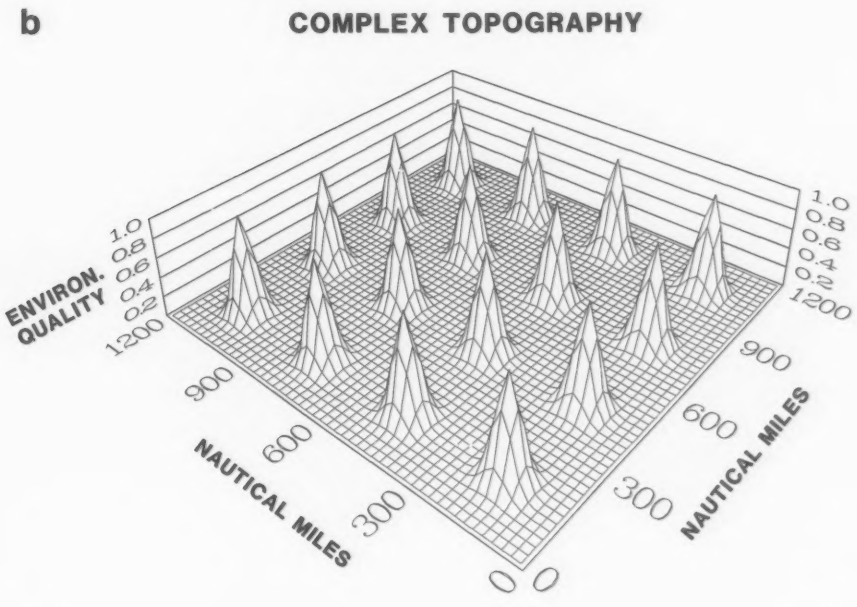
mental topography, representing a 300 mile gradual gradient from "best" to "worst" conditions (Fig. 2a). In the complex, steep environment the precipitous slopes generate a distance of only about 75 miles between maximum and minimum values for environmental quality, the slopes being separated by a "desert" of unfavorable habitat about 150 miles wide (Fig. 2b).

These two topographies were chosen to *bracket* a range of reasonable possibilities for patterns in environmental characteristics that may cause nonrandom clustering of dolphin schools. The factors of peak gradient and peak spacing (number of peaks) are confounded here because we tested only the two topographies, simple:gentle and complex:steep. Gentle gradients are confounded with few peaks; steep gradients are confounded with many peaks. We did not test the other two possibilities (simple:steep and complex:gentle) because these are both intermediate topographies that would have generated intermediate results. In the interest of simplicity, we restrict this simulation study to the two extreme cases.

The rate at which the topography moved (1 knot) was chosen to simulate movement of major habitat features affecting dolphin school movements. Because direct identification and measurements of such features have yet to be made, the choice of rate was based on reported speeds of major ocean currents in the eastern tropical Pacific and apparent seasonal movements of major concentrations of dolphin schools. Reported current speeds include 0.1 to 0.3 knots for the core of the Pacific North Equatorial Current bordering the fishery area on the north (Seckel 1975), 1.2 to 2.4 knots for the equatorial undercurrent underlying the fishery area (Wyrtki 1966), and 1.2 to 2.4 knots for maximum speed of the Equatorial Countercurrent surface waters encompassing a majority of the fishing area (Wyrtki 1966). School sightings data from research ships indicate that major concentrations of dolphin schools may move seasonally between distant areas at approximately 0.3 knots (200 nmi/mo)[8].

Our choice of 1 knot was based on the assumption that the mechanism(s) responsible for aggregating dolphin schools are most probably related to distributions of prey and water mass signatures indicating presence or absence of the prey. Dolphins in the ETP consume small (10–50 cm) fish and squid (Perrin et al. 1973). This mobile prey base will in turn be responding to

[8]S. B. Reilly, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1987.



topography (a) and the complex topography (b).

movements of its own prey base of smaller animals. We reasoned that it is unlikely that this food chain is being swept along as rapidly as the maximum current speeds, but, especially on smaller scales, the distributions of prey and predator are probably moving faster than the speeds apparently characteristic of large-scale seasonal movements. We chose 1 knot as a conservative approximation. It is possible that dolphin aggregating mechanisms move, overall, more slowly than 1 knot, but probably not faster. Thus by comparing simulation results from nonmoving topographies versus topographies moving at 1 knot, we have tried to bracket the range of responses likely to occur in the real system.

In our model, dolphin schools were made to respond to these topographies by adjusting their *speed* according to the quality *level* and by adjusting their *direction* according to the gradient in quality experienced during the previous time step. The range of speeds chosen for dolphin schools (0.5 to 2.4 knots) was based on average observed cruising speeds of dolphin schools in the ETP[9]. In the model, dolphin speed is fastest at the lowest quality levels and slowest at the highest quality levels. Direction choice is stochastic with probabilities biased in the forward direction when the gradient is positive (conditions improving) and in the reverse direction when the gradient is negative (conditions deteriorating). Thus the rules for school speed and direction cause schools to circle slowly in "favorable" areas (i.e., on the peaks) and to move rapidly straight ahead in "unfavorable" areas (i.e., the valleys between peaks).

Vessel movements were controlled by each vessel's history of dolphin school sightings, through a "sightings memory" variable. The value of the variable increases by one unit each time a school is sighted and it decays constantly by a given proportion with each time step. Thus, the value of the variable will be high when a vessel is in a "good" area (i.e., has seen lots of schools) and will be low when the vessel is in a "bad" area (schools are few). Vessel direction is stochastic and affected by the value of this "sightings memory" variable. When the value is high, direction choice is biased in the reverse direction; i.e., the vessel is most likely to turn approximately 180 degrees. When the value is low, small angles are much more likely to be chosen; i.e., the vessel will tend to continue moving forward. Each vessel maintains its own sightings variable independent of the sightings variables of other vessels, so that each vessel moves independently of all other vessels.

Generation of Simulated TVOD

Each simulation began with totally random distributions of both vessels and dolphin schools. Nonrandom spatial distributions of vessels and schools then developed as a function of the environmental topography and of the movement rules for schools and vessels. Each simulation continued for 600 time steps of 1 h/step.

Estimates of school abundance were based only on TVOD collected during the last 200 steps. By this time, the model had in all cases settled into a quasi-steady state (Fig. 3). TVOD for each vessel, collected during each of these last 200 steps, included vessel number, total number of miles searched during that step, position of the vessel at the end of the step, and presence or absence of a school sighting. Only one school could be sighted per vessel per time step.

TVOD were "collected" for all dolphin schools moving within 2 nmi of any vessel. Two nautical miles is the effective strip width found commonly with line transect analyses of real TVOD.[10] All vessels were assumed to carry observers. Observers were always on duty collecting data (i.e., were never "off effort"). Vessels searched continuously (i.e., did not stop at "night").

Data Analyses

TVOD were aggregated subsequently into 1° squares prior to abundance estimation. One-degree squares are the smallest geographic subdivision that retains, with real TVOD, sufficient data for line transect analysis (Polachek 1983; Buckland and Anganuzzi 1988).

Four replicated simulations were conducted for each of eight different cases representing two

[9]Hedgepeth, J. 1985. Database for dolphin tagging operations in the eastern tropical Pacific, 1969–1978, with discussion of 1978 tagging results. Admin. Rep. No. LJ-85-03. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[10]M. Hall, Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun.

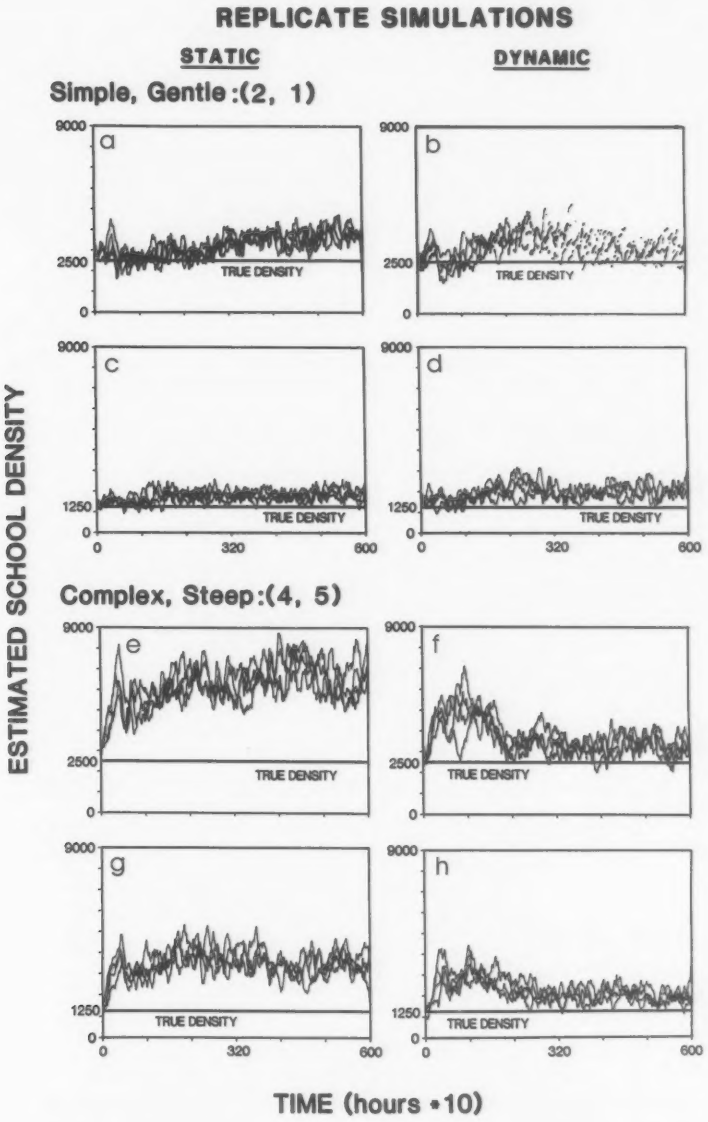


FIGURE 3.—Time course of total school abundance estimates derived from unstratified TVOD. Estimates were derived during each of 600 time steps for 4 replicated runs of 8 different starting conditions. The cases differed in environmental topography (simple, gentle vs. complex, steep), in whether the topography was static or dynamic (sliding left at 1 knot), and in underlying abundance of dolphin schools (1,250 or 2,500). Numbers in parentheses (2, 1; 4, 5) are parameters used in the equations generating the topographies.

levels for each of three factors. The factors and levels included 1) complexity of the environmental topography (simple, with 4 gently sloping peaks vs. complex, with 16 steeply sloping peaks), 2) topography dynamics (static vs. moving at 1 knot) and 3) dolphin school abundance (2,500 vs. 1,250 schools). Topography movement was implemented by causing the grid

of peaks and valleys to slide uniformly sideways from "right" to "left".

Stratification Schemes

TVOD collected under each of the eight cases were subjected to three types of stratification: 1) none, 2) raw encounter rate, and 3) smoothed encounter rate.

In the case of no stratification, school abundance was estimated simply as

$$(TE/AS) * (TA) \quad (1)$$

where TE is total number encounters by all vessels during time steps 400 to 600, AS is total area searched during that time, and TA is total area simulated (1,200 × 1,200 nmi). In this case, all 1° squares were treated as a single group or stratum.

In stratifying by raw encounter rate, encounter rates (schools encountered per nautical miles searched during the last 200 time steps) were calculated for each 1° square. The squares were subsequently ranked in ascending order of encounter rate, and grouped into (n) strata. Strata were demarcated on the basis of including at least (m) schools (encounters) per stratum. Both (n) and (m) were calculated using an algorithm developed by the Inter-American Tropical Tuna Commission for their line transect analyses of dolphin abundance in the ETP (Buckland and Anganuzzi 1988). School abundance was then estimated for each stratum separately. Total school abundance in the entire 1,200 × 1,200 nmi area was then estimated simply as the sum of these estimates per stratum.

In stratifying by smoothed encounter rate, encounter rates in each 1° square were smoothed according to the algorithms developed by Buckland and Anganuzzi (1988). Squares were then ranked and assigned to strata based on these smoothed encounter rates. This smoothing algorithm generally creates strata composed of contiguous areas of squares, arrayed in decreasing order from area of apparent high density to areas of lower density. It is not uncommon, however, for some squares in a given strata to be scattered in areas isolated from the majority for that stratum.

The smoothed encounter rates generated by the algorithm were used only during this stratification step; school abundances were estimated for each stratum using the raw (actual) encounter rate. Total abundance of dolphin schools was then estimated as the sum of the estimates for each stratum.

Estimates Derived

Two types of estimates were derived from these simulated TVOD: *total* abundance of dolphin schools in the entire simulated area, and *change* in school abundance from one sampling period to another, where this change was estimated simply as the ratio of school abundance estimates derived under two different sets of initial conditions in the model. Thus, school abundances were estimated first, and change estimates derived subsequently from these abundances. These estimates of change were calculated as a very simple analogy to a trend estimate, extending in this case over two sampling periods instead of over series of estimates. This two-sample change estimate is only a rough approximation to a trend estimate derived from a series of measurements (Gerodette 1987). However, conclusions about the effects of inconsistent biases on this *change* estimate will be valid for *trend* estimates also, except for the unlikely case in which effects of various inconsistent biases cancel each other out, so that the trend estimate reflects the actual trend, but only fortuitously.

Change estimates were derived under two conditions. Under the first condition the estimate was simply the ratio of the abundance estimate when true density was 1,250 schools (low density) to the estimate when the true density was 2,500 schools (high density). All other conditions in the model remained the same. This simulates the situation of consistent biases.

Under the second condition, the trend estimate was the ratio of one low-density estimate to one high-density estimate, but the ratio was constructed by selecting abundance estimates from cases which differed in other factors in addition to differing in dolphin abundance. This simulates the situation of biases being inconsistent from one sampling period to the next. Three ratios were selected from the many possibilities, to simulate three reasonable scenarios in the real ETP and to bracket a range from mild to severe inconsistencies.

The first of the three ratios was an estimate of abundance change in the simple environment, where in one case the environment was static during the sampling period and in the other the environment was moving at 1 knot. The second

ratio was an estimate of abundance change coupled with a change in the environment from simple to complex (environments remaining static in both cases). The third ratio was an estimate of abundance change coupled with a change from a simple and static environment to a complex and moving environment. These three cases simulated ratio estimates of abundance changes from, for example, one year to the next, where conditions in the environment have also changed between years.

RESULTS

Development of Nonrandom Distributions

Relatively similar dynamics occurred within the four replicated runs of each of the eight cases (Fig. 3). In all cases, nonstratified estimates of total school abundance, calculated for each of the 600 time steps, developed progressively positive biases. Early during each simulation, estimates were relatively accurate. But as schools and vessels became progressively nonrandomly distributed (Fig. 3a–h), estimates deteriorated owing to the concentration of search effort by tuna vessels in the areas where dolphin school were prevalent and to the concomitant avoidance by vessels of areas with few schools.

Although positive bias developed in all cases, the degree and progression of bias was strongly influenced by environmental topography, both configuration and dynamics. Relatively little bias developed in cases where the topography was relatively noncomplex (Fig. 3a, c) or was moving at 1 knot (Fig. 3b, d, f, h). Very large biases developed in cases where the topography was complex and static (Fig. 3e, g).

School Abundance Estimates

Nonstratified estimates of total school abundance, calculated from TVOD collected during the last 200 time steps, show the positive bias indicated in the time courses shown in Figure 3. The degree of positive bias in unstratified estimates was not constant, but varied with model conditions (Fig. 4). Bias was least for the case of a simple, moving environment, slightly higher for the complex, moving environment, slightly higher again for the simple, static environment, and dramatically higher for the complex, static environment.

Estimates of school abundance based on stratification by raw encounter rate were in all cases relatively accurate, although estimates tended to be negatively biased for the cases of a simple environment (Fig. 4).

Estimates based on stratification by smoothed encounter rate also tended to be negatively biased for the cases of a simple environment (Fig. 4). The case of a complex, moving environment led to a slight positive bias in abundance estimates. But the complex, static environment led to pronounced overestimates of abundance that rivaled results from the unstratified analyses.

Reducing the underlying density of schools by half, from 2,500 to 1,250 schools, was mirrored by decreases of approximately one half in school abundance estimates (Fig. 4). Patterns of over- or underestimation under various model conditions remained consistent over both densitites. For example, the most severe bias occurred in both cases under conditions of a complex, static environmental topography.

Change Estimates

When change estimates were derived by comparing cases in which only the underlying density of schools was changed (i.e., when biases remained consistent between sampling periods) the estimates based on raw or smoothed encounter rate stratification were very accurate (Fig. 5). Estimates based on unstratified data were strongly biased but analyses of real TVOD are never conducted on unstratified data, so this case is useful only as an indication of improvement in estimation achieved by stratifying.

Inconsistent biases produced a dramatically different result. Even relatively small changes in underlying model conditions produced moderate to large biases in the change estimates. Also, these biases were neither consistently positive nor consistently negative, even within a single set of comparisons (Fig. 5).

DISCUSSION

School Abundance Estimates

Stratification

Overestimates were derived from nonstratified data in all cases because vessels (and therefore observers) spent more time (expended more effort) in areas where dolphin schools were abun-

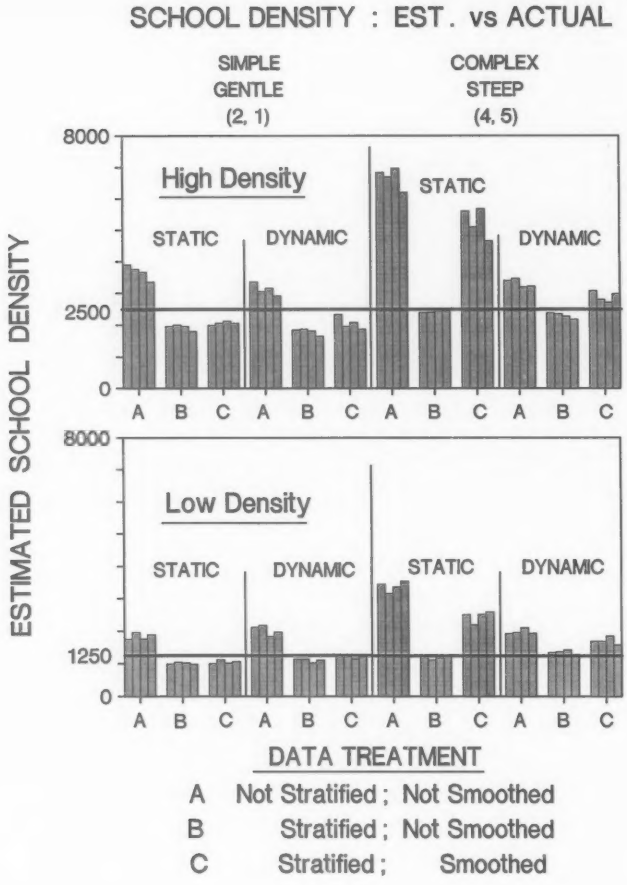


FIGURE 4.—Estimated vs. actual school density (total number of schools in simulated area) under 8 different cases for model conditions and under 3 types of data simulation for each condition. Each set of 4 columns is a set of 4 replicated runs for a given case. The cases differed in 1) environmental topography (simple, gentle vs. complex, steep), 2) whether the topography was static or dynamic (sliding left at 1 knot), and 3) actual abundance of dolphin schools (1,250 or 2,500). Numbers in parentheses (2, 1; 4, 5) are parameters used in equations generating the topographies. Two and 4 refer to the number of peaks arrayed along each axis of the spatial plane, generating a regular square grid of peaks. One and 5 are values of the parameter controlling peak slope; 1 generates a gradual slope, 5 generates a precipitous slope. Heavy lines across the figures indicate the true density (abundance) of schools in each set of simulations. Data treatments include A) no stratification before estimating school abundance, B) stratification of 1° squares based on observed (raw) encounter rates per square, and C) stratification of 1° squares based on smoothed encounter rates per square.

dant, and avoided areas where schools were few (Fig. 6). Overestimates of average school abundance per 1° square resulted from this pattern of effort because few samples from low density squares contributed to the average. Overestimates of total school abundance then followed directly by extrapolating this overestimate to the entire area.

Overestimation of school abundance was especially pronounced for the case of a complex,

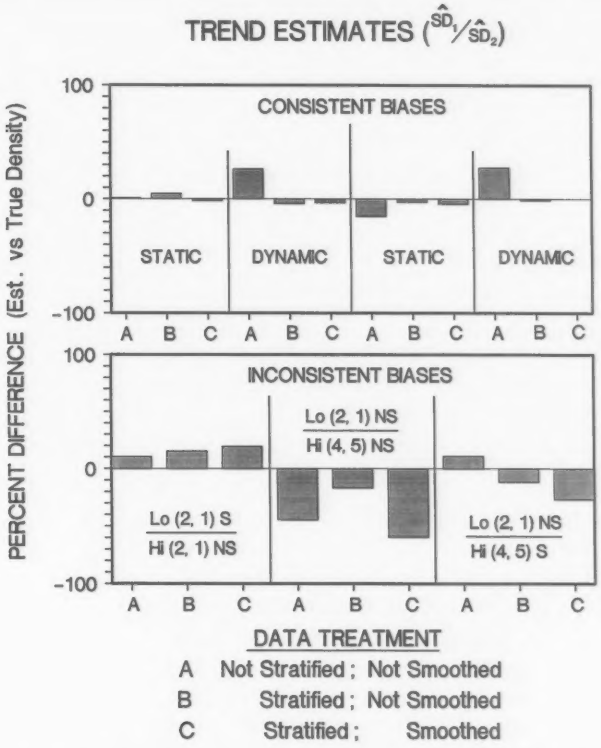


FIGURE 5.—Comparisons of estimated versus actual change ("trend") in school abundance from one sampling period to another. Changes in abundance were estimated as the ratio of school abundance (estimated or actual) under one set of model conditions (SD_1) to school abundance (estimated or actual) under some other set of conditions (SD_2). Lo and Hi refer to actual abundance of schools (Lo = 1,250 schools, Hi = 2,500 schools). S and NS refer to topography dynamics (S = topography sliding sideways at 1 knot (dynamic), NS = static topography). Number in parentheses refer to parameters generating topographies. Two and 4 refer to number of peaks along each axis. One and 5 refer to peak gradient (1 = gradual slope, 5 = precipitous slope). Three change estimates, resulting from three different types of data stratification, were generated for each comparison: A) no stratification before estimating school abundance, B) stratification of 1° squares based on observed (raw) encounter rates per square, and C) stratification of 1° squares based on smoothed encounter rates per square. Comparisons are expressed as (1 – (Estimated change/actual change))*100, so that differences appear as percentages. Differences are 0 when estimated changes equal actual changes.

static environment because this condition led to very concentrated clumping of schools within a few 1° squares. Vessels concentrated most of their effort in these few squares with very high density. Overestimates were less pronounced in the cases of a simple environment because here the areas of higher density were much more diffused and not so different from areas of low density. The gradient of increasing density toward the topographic peaks built up much more slowly, so that vessels sampled many more squares with relatively low density than had been the case for the complex, static environment. The overestimate of abundance was relatively lower for the case of the complex, dynamic environment for essentially the same reason; the

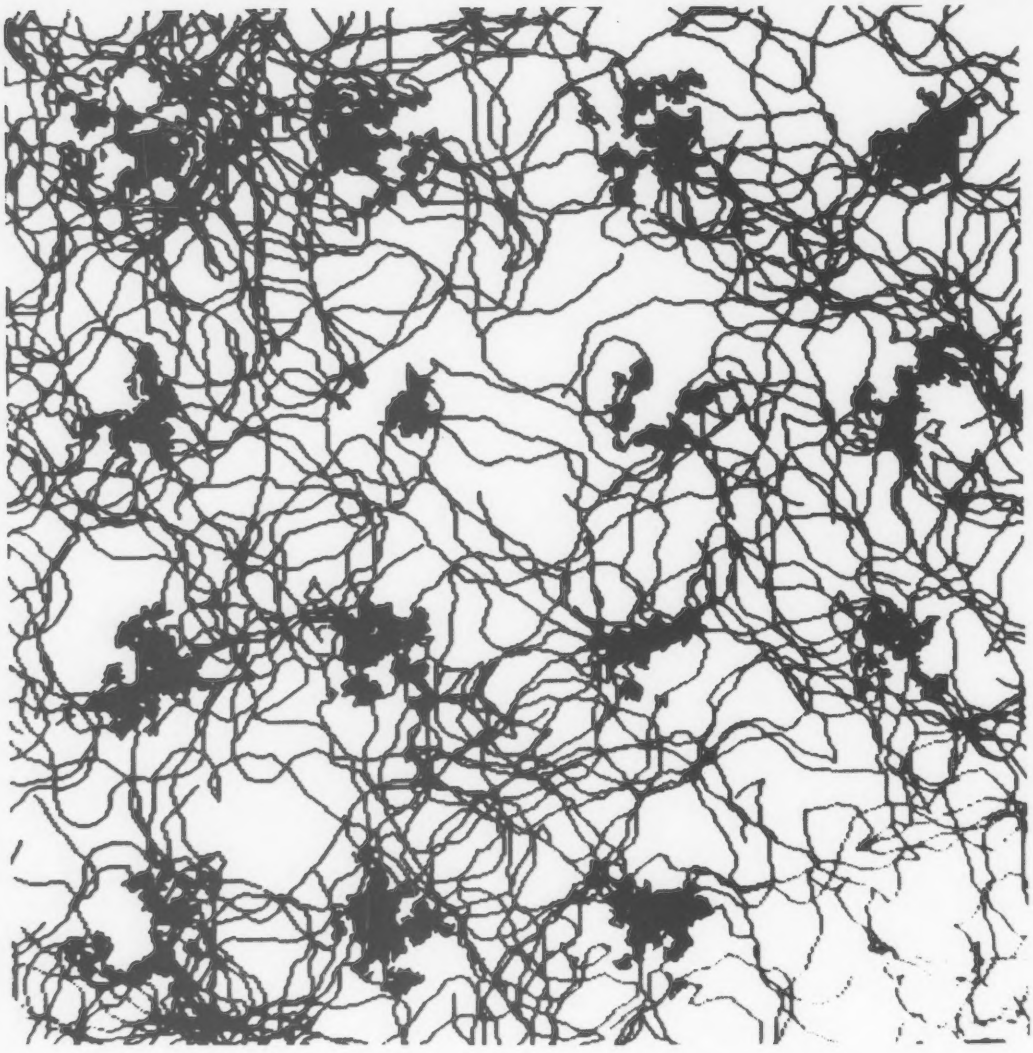


FIGURE 6.—Tracks of simulated purse seine vessels after 400 time steps during a simulation with a complex, static environmental topography. Vessel movements are concentrated near peaks in the topography, in response to the high density of dolphin schools in these areas.

characteristics of the environment produced many more squares with relatively low densitites. But here the process generating these relatively low-density squares was very different from the simple environment case. In the complex, moving environment the peaks were moving at 1 knot. Aggregating the data from the last 200 time steps generated a smeared version of the underlying 16-peak array. Integrated over the entire period of data collection, the areas of dolphin concentration appear as bands across the simulated area, rather than as individual peaks (Fig. 7). The dolphin schools spread themselves out over a larger number of squares than in the static case, producing lower estimates of average density per square.

Stratification By Raw Encounter Rate

Estimates derived from stratification by raw encounter rate were relatively unbiased in all cases because in these simulations we "collected"

an unrealistically large number of TVOD with unrealistically complete coverage of the simulated area. Of the four hundred 1° squares in our 1,200 × 1,200 nmi area, no more than six went unsampled during any simulation. As a result, encounter rates in each square reflected very accurately the true school density in each square. Stratifying by these encounter rates, deriving a different estimate of average school density for each stratum, taking the weighted average of these estimates, and then extrapolating this weighted average to the entire area produced quite accurate estimates of total school abundance.

The slight negative bias in the cases of a simple environment may be due to a curious effect that was not obvious until we made a movie of vessel and school movements generated by TOPS for a simulation of the simple moving topography. It appears in this movie that vessels tend to undersample the areas of highest density in the center of the gradual peaks, because the vessels encounter enough schools along the periphery to keep them from turning into these high density, central areas. Undersampling the highest densities of course will lead to an underestimate of the average density per square and thus to an underestimate of total abundance.

This avoidance of peak centers did not occur with the complex, static environment used in our simulations, apparently because most of the peak area in this topography occurred within only a few squares (Fig. 2b). Vessel speed was apparently sufficient to carry most vessels into the highest density areas before the effects of sightings caused the vessels to slow down.

Stratification by Smoothed and Interpolated Encounter Rate

Given the apparent accuracy of estimates derived under the stratification by raw encounter rate, it would seem irrelevant to proceed to the more complicated and sometimes ineffective stratification by smoothed encounter rates. However, real world tuna vessels never sample the ETP as completely as the simulated vessels sampled the TOPS environments. In most years, fewer than half the vessels carry observers, the fleet as a whole samples less than half the entire ETP, and the sampling that is done tends to be concentrated seasonally in variable geographic areas (Buckland and Anganuzzi 1988). This leaves many 1° squares unsampled.

For management purposes, we cannot assume that squares with no effort contained no dolphins; therefore, we are left with the necessity of estimating densities in those unsampled areas. We have to fill in the holes somehow, so an interpolation method, either a more robust method than used to date, or some new method, is required.

In most of the TOPS simulations, Buckland and Anganuzzi's (1988) smoothing and interpolation routines worked quite well, with accuracy rivaling that of the raw encounter rate stratification. The very poor performance of the smoothing algorithm in the case of a complex, static environment, however, is troubling because we have no data from the field to determine whether or not such topographies exist in the ETP. We suspect that such topographies do exist because the parameters used in the TOPS model were chosen specifically to be reasonable. In particular, the distances between peaks were chosen to bracket the apparent distances between clusters of dolphin schools as indicated by sightings from research vessels.[11] Also, the movement rates by vessels, schools, and topography were specifically selected to approximate observed rates.

The severe bias in the complex static case arises owing to an interaction between the effective sampling frequency (in this case, 1° squares), the peak topography, and the mechanics of the smoothing algorithm. The algorithm works by calculating, for each square, a smoothed encounter rate that is a weighted average of encounter rates for all squares within a radius of at least four squares. Thus the smoothed rate in each square is affected by rates across a diameter of at least eight 1° squares, or a distance of at least 480 nmi (8 × 60 nmi). In the case of the complex, static topography, this minimum distance is greater than the distance between peaks (300 nmi). Also, the relatively precipitous peaks encompass only 3 or 4 squares and are separated by low-density areas several squares across. The smoothing algorithm tends to "fill in" these low-density areas, elevating apparent encounter rates in the intervening squares and causing squares to be assigned to strata out of proportion to the true densities of dolphin schools in the squares.

It is possible that the relatively precipitous slopes of the peaks in the complex environment

[11]R. S. Holt, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1987.

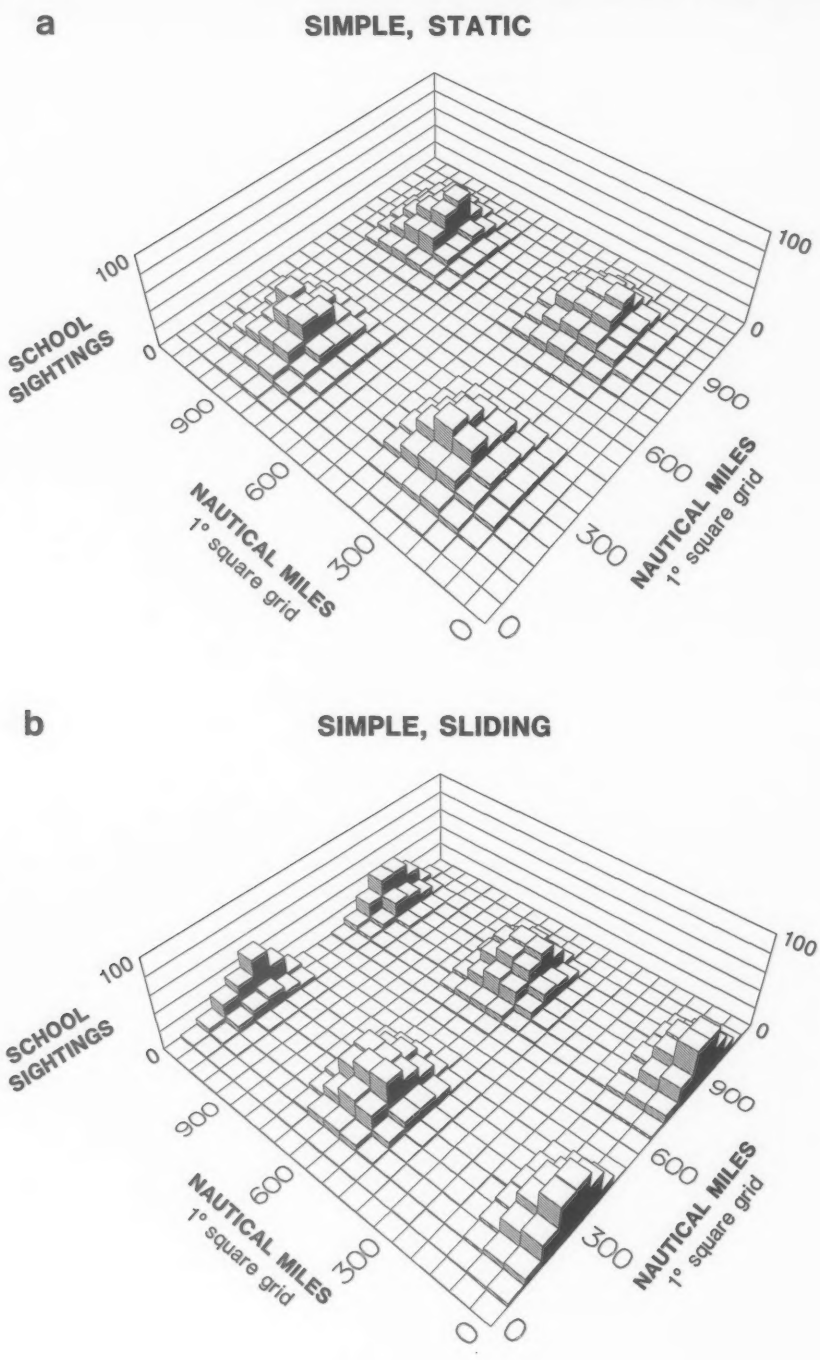
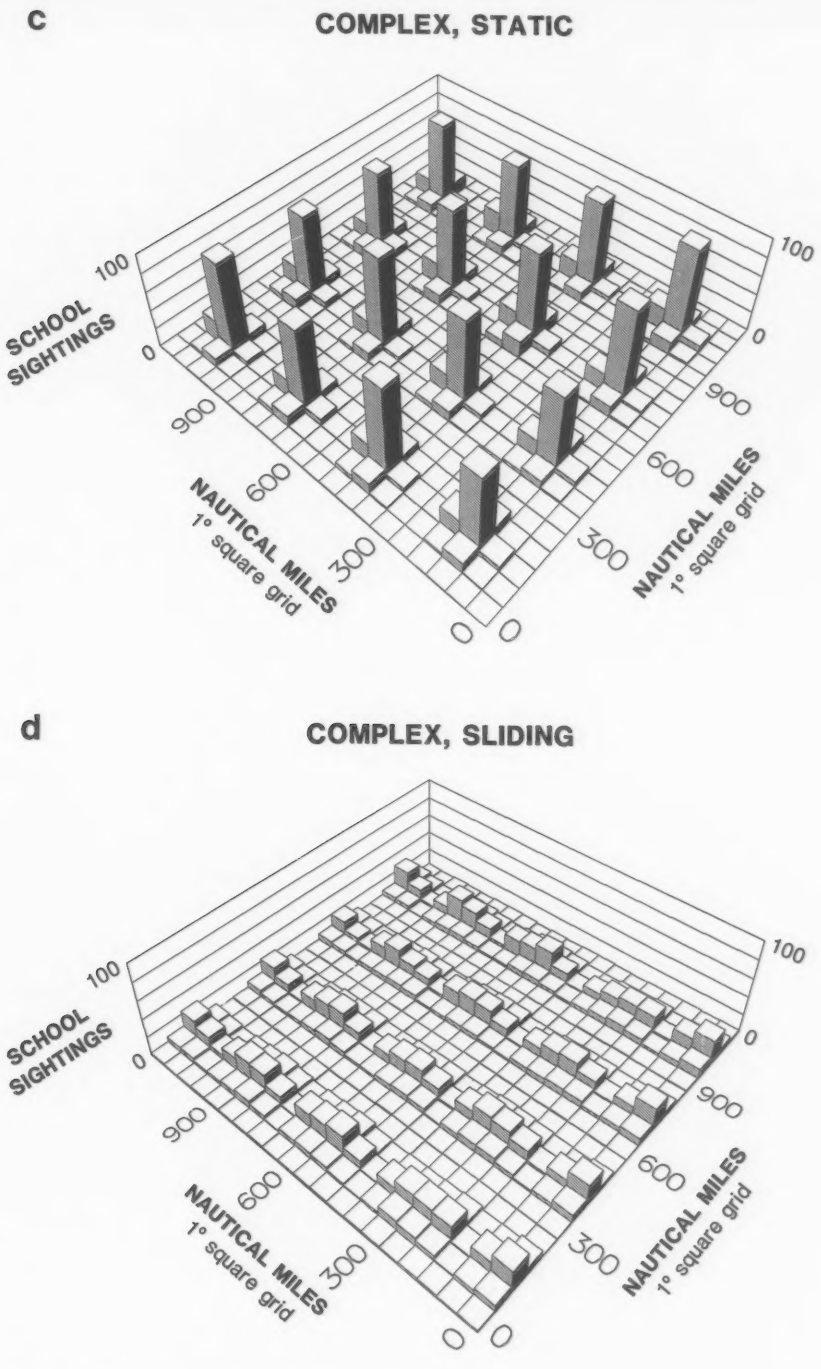


FIGURE 7.—Average number of sightings of dolphin schools per 1° square during the last 200
a) simple, static, b) simple, sliding,



time steps of one simulation for each of the four types of environmental topography
c) complex, static, and d) complex, sliding.

are unrealistic, but in fact these slopes extend over at least two 1° squares (Fig. 2b). This is a distance of at least 120 nmi. Conditions change across ocean fronts in distances much shorter than this, and ocean fronts are aggregating mechanisms for many marine biota (Owen 1981). Of course, such fronts are never static and the smoothing algorithm worked quite well in the complex, dynamic environment, apparently owing to the smearing effect discussed previously. However, as in the previous case, we have as yet insufficient data to identify the conditions actually pertaining in the real ETP.

The major point is that the simulations have shown that clustering characteristics on relatively small scales (10s to 100s of miles) can seriously bias estimates of abundance derived via the smoothing algorithm, which is a problem because as yet we know almost nothing about clustering on this scale in the real ETP. The model results indicate strongly that future research should be focused either on resolving this lack of information or on developing alternative analyses that are not as sensitive as this smoothing algorithm to these small-scale spatial effects.

Change Estimates

These demonstrated problems with estimating school abundance are serious but in real-world analyses could perhaps be ignored; the next set of dolphin quotas will be determined not on the basis of estimated absolute abundance at some point in time but rather on the basis of *estimated changes* in abundance (Holt et al. 1987). This is an advantage in the estimation process because as long as nothing other than dolphin abundance changes from one sampling period to the next (i.e., as long as biases remain consistent), then accurate estimates of those changes in abundance can be derived from TVOD.

However, we know almost as little about whether biases truly remain constant (consistent) in the ETP, as we know about small-scale spatial distributions of dolphin schools. It is obvious from Figure 5 that even relatively small changes in bias can lead to considerably inaccurate estimates of change and, by implication, estimates of trend. A change as simple as moving from a static to a slowly moving environment produced an overestimate in the ratio estimate of almost 20% (Fig. 5, Lo(2, 1)S/Hi(2, 1)NS). Not even the direction of bias remained consistent, changing from positive in some cases to negative in others.

The ratio estimate based on a simple static environment during one sampling and a complex static environment during the other period (Fig. 5) is of particular interest, because an effect of this type may be the basis for the anomalous and biologically unlikely dip in Buckland and Anganuzzi's (1988) estimates of abundance for northern offshore spotted dolphin, *Stenella attenuata* during 1983 (Fig. 8), the year of an exceptionally strong El Niño. Our simulation results in this case lead to a potentially testable hypothesis about a factor that may have significantly affected analyses of real TVOD. Preliminary analyses of apparent differences in distributions of dolphins during El Niño versus non-El Niño years support the hypothesis that changes in spatial distributions led to inconsistent biases and thus to inaccurate trend estimates during these years.[12]

SUMMARY

The results from these simulations are useful in a general sense; they show that significant biases can develop within the simple model structure used here. The quantitative results are specific to the parameter values and movement rules chosen for these particular simulations and are neither intended nor assumed to mirror specific distributions of either vessels or dolphin schools in the real environment of the ETP. Although parameter values controlling rates and abundances are "correct" to the best of our knowledge, choosing different parameters for the functions controlling dolphin responses to the environment, or vessel responses to dolphins, would probably change both the rates and spatial characteristics of pattern development and thus estimates of abundance derived.

Other clustering patterns could have been used, and other results generated. However, our purpose at this stage was not to generate a catalogue of patterns and responses. Our purpose was to test the effects of varying a simple but reasonably realistic (in terms of rates and spacings) aggregating pattern for dolphin schools, using the results to determine whether any insight could be gained into the problem of estimating abundance of dolphin schools in the real world, using real TVOD.

Indeed, we found that our simplified simula-

[12]S. B. Reilly, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun.

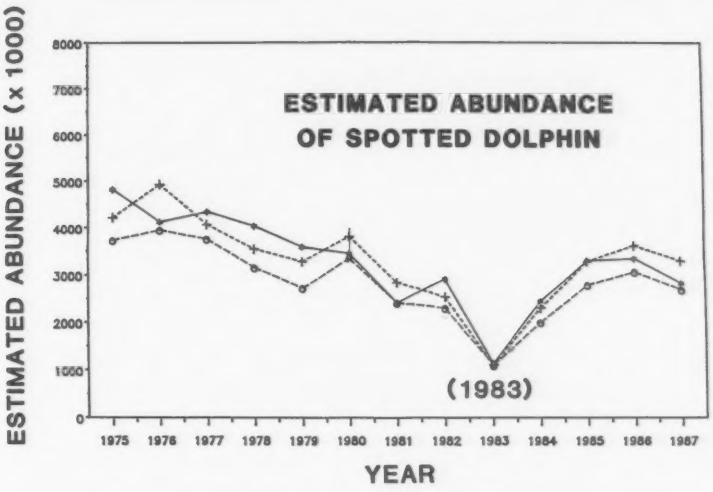


FIGURE 8.—Estimated abundance of northern offshore spotted dolphin, *Stenella attenuata*, showing biologically unlikely recovery in 1984 following apparent decrease in abundance during 1983 (from Buckland and Anganuzzi 1988).

tion approach identified two critical problems that must be addressed if TVOD are to an effective source for estimates of dolphin abundance or changes in abundance in the eastern tropical Pacific Ocean. These critical problems are 1) the effect of small-scale nonrandomness of dolphin schools, and 2) the interactions between these small-scale patterns (sampling frequency and smoothing algorithms) on estimates of school abundance or change in abundance derived from line transect analysis of sightings data. Research effort should now be directed toward identifying and characterizing school distributions within these smaller spatial (and temporal) scales, and toward improving the efficacy of existing methods or developing new methods for analyzing TVOD.

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Maturation and Reproduction in Two Hawaiian Eteline Snappers, Uku, *Aprion virescens*, and Onaga, *Etelis coruscans*

Alan R. Everson, Happy A. Williams, and Bernard M. Ito

ABSTRACT: Size at sexual maturity, spawning season, and pattern of egg release were determined for two of Hawaii's commercially important snapper species: uku, *Aprion virescens*, and onaga, *Etelis coruscans*. Sexual maturity of females was assessed by macroscopic and microscopic (oocyte measurement and histology) techniques and gonosomatic indexes. Interspecific differences were noted in many aspects of the reproductive biology. Both species had protracted spawning seasons: uku spawned in May-October while onaga spawned in June–November. Female size at sexual maturity was 425–475 mm fork length (FL) for uku and 675–725 mm FL for onaga. Both species were determined to be multiple spawners, although the number of batches spawned per season could not be established.

Uku, *Aprion virescens*, and onaga, *Etelis coruscans* (Lutjanidae), are species of considerable importance in terms of total landings and value to bottom fish fisheries in southern Japan (Masuda et al. 1975), Guam, the Northern Marianas (Amesbury and Myers 1982), Vanuatu (Brouard and Grandperrin 1985), American Samoa (Western Pacific Regional Fishery Management Council (Council) 1986), and Hawaii (Ralston and Kawamoto[1]). In addition, many other Pacific island nations have subsistence and commercial fisheries for these species. In Hawaii, uku and onaga ranked second and third, after *Pristipomoides filamentosus*, in total catch and value among bottom fish species in 1984 (Pooley 1987).

Both species are widely distributed throughout the tropical Indo-Pacific. Uku range from East Africa to Hawaii and from southern Japan to Australia (Allen 1985), and onaga extend to the Atlantic coasts of South America and Africa (Druzhinin 1970). Uku are caught at the surface by trolling gear and at ≤ 300 m depths by deep-sea handline gear (Druzhinin 1970), whereas onaga are restricted to deeper waters between 220 and 320 m. In Hawaii, the greatest portion of the uku and onaga catches comes from the Penguin Bank region, which is southwest of Molokai in the main Hawaiian Islands (Ralston[2]).

Relatively few reproductive studies have been completed for the commercially important bottom fishes of the western Pacific, even though such information represents a critical component of the biological basis of management for the bottom fish and seamount groundfish fisheries in this region (Council 1986). Some information is available on Hawaiian stocks of *P. filamentosus* (Ralston 1981; Kikkawa 1984), *Etelis carbunculus* (Everson 1984), and *Seriola dumerili* (Kikkawa and Everson 1984), but none is available for uku and onaga. Thus, a study was undertaken to determine the size at sexual maturity, spawning season, and pattern of egg release of uku and onaga. Size at sexual maturity is a particularly important parameter used to assess and evaluate the impact of fishing mortality on spawning stock biomass and to determine levels of optimum fishery yield (Polovina 1987). During this study, we also attempted, within the constraints imposed by our sampling program, to develop an efficient method for determining gonad maturity. A third goal was to discern interspecific differences between the reproductive biology of the two species and to interpret those differences.

[1]Ralston, S., and K. E. Kawamoto. 1987. An assessment and description of the status of bottom fish stocks in Hawaii. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-87-7, 55 p.

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Fishery Bulletin, U.S. 87: 877–888.

[2]Ralston, S. 1979. A description of the bottomfish fisheries of Hawaii, American Samoa, Guam, and the Northern Marianas. A report submitted to the Western Pacific Regional Fishery Management Council, Honolulu, 102 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu HI 96822–2396.

MATERIALS AND METHODS

Uku and onaga caught in 1984–86 and 1985–87, respectively, by commercial fishermen using deep-sea hook-and-line gear were weighed and measured for fork length (FL), and their capture locations were noted. Most were caught in the main Hawaiian Islands and were sold through the Honolulu wholesale fish auction. Following sale of the fish, viscera were extracted by the purchasing agent and refrigerated with an identifying tag. Gonad samples were collected later and preserved at the laboratory either in modified Gilson's fluid (Bagenal and Braum 1968) or Bouin's fluid.

Sexual maturity of females was evaluated by several methods. First, ovaries were staged macroscopically and given a preliminary maturity stage designation (Hilge 1977) (Table 1). To refine and confirm these macroscopic designations, at least one of the following three additional microscopic techniques was used: volumetric or cork borer subsampling, which is based upon the size and appearance of individual oocytes, or standard histological examination. Hilge's (1977) table was also used to assign a final stage designation to these ovaries. To avoid confusion, prespawning adults prior to vitellogenesis were classified as stage I immature, and prereproductive individuals as stage I juvenile.

To determine oocyte size-frequency distributions by volumetric subsampling, uku ovaries preserved in modified Gilson's fluid were examined. After adequate time for dissolution, connective tissues were removed, and the remaining "free" ova were placed in a flask, which was then filled with 200 mL of water. A homogeneous distribution of ova was obtained by using a magnetic stirrer (Van Dalsen 1977). A 3 mL sample was then pipetted onto a gridded petri dish and examined under a binocular dissecting scope at 50×. With an ocular micrometer, 100–200 oocytes were measured along their longest dimension. This method precluded the need to measure oocytes from various sites within the ovary to determine spatial homogeneity of development. Maturity stages were assigned based upon the largest oocyte mode and the degree of oocyte transparency (Table 1).

Subsamples of ovaries of both species preserved in Bouin's fluid were taken from the anterior portion with a cork borer and examined under a binocular dissecting microscope at 50×. The average diameter of the largest oocyte mode was determined, and the percentage of each maturity stage present was noted. Oocyte diameter frequency plots were constructed for uku ovaries in various stages of development and compared with similar plots constructed by using oocyte diameter data obtained by the volumetric method.

For histological examination, some ovaries of both species representing various visually identifiable maturity stages were transferred from Bouin's fluid to 70% ethanol. Portions of ovaries from 28 uku and 22 onaga caught at various times of the year were embedded in paraffin, sectioned at 5 μm, stained with hematoxylin, and counterstained with eosin. Each was as-

TABLE 1.—Ovary developmental stage designations used for study of the reproductive cycle of uku and onaga. Designations are adapted from Hilge (1977).

Class	Stage	Oocyte developmental status	Gonad external appearance	Stage classification criterion
I	Immature	Oogenesis from oogonium to primary oocyte with cytoplasmic vacuoles beginning to appear	Genit ridge to definite gonad; individual eggs not discernible	Oogonia transparent; primary ooctes translucent
II	Developing	Vitellogenesis	Elongation of the ovary	Opaque yolked oocytes
III	Ripe	Hydration	Swollen; ovary wall thin	Transparent, ripe ova
IV	Spent	Atresia, general cell breakdown	Slack; shrinking ovary; ovary wall thick	Residual ova

signed a maturity stage based on the criteria in Table 1. Oocytes were histologically identified using information provided in Crossland (1977). Sectioned ovaries also were examined for the presence of postovulatory follicles and oocyte atresia, features used to establish criteria for the estimation of spawning frequency and to separate juveniles from prespawning adults for determination of size at sexual maturity (Hunter and Macewicz 1985).

The results of these four visual methods were compared with gonosomatic index (GSI) values [(gonad weight/body weight) × 100]. Gonosomatic indexes were calculated for both species to provide a rapid but preliminary indication of developmental stage, although an insufficient number of uku testes were obtained. Excluded from this analysis were individuals that had not yet reached size at sexual maturity. Spearman's coefficient of rank correlation (Snedecor and Cochran 1978) was used to ascertain whether a positive relationship existed between GSI and maturity stage during the spawning periods for females of each species.

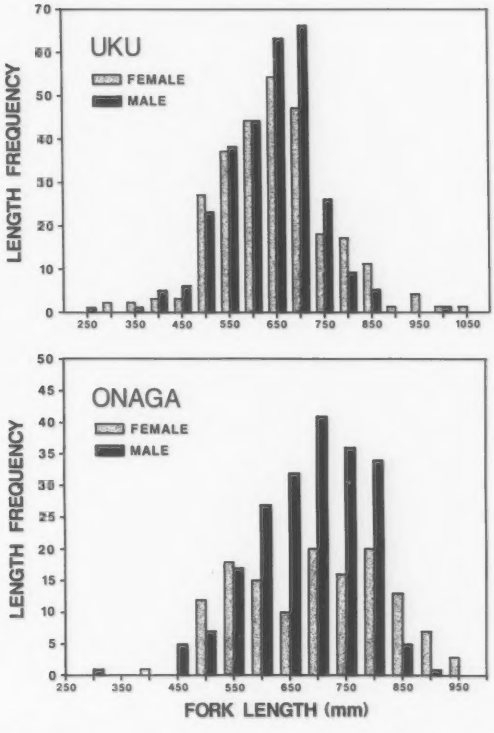


FIGURE 1.—Length-frequency distribution of male and female uku and onaga.

Size at sexual maturity (L_{50}) was defined as the smallest length category in which at least 50% of the individuals were mature (i.e., stage II or beyond, GSI > 1.5) during the spawning season. The logistic equation was fitted to the percentage of mature individuals in each size class (P_x) and FL (Gunderson et al. 1980; Ni and Sandeman 1984); that is

$$P_x = \frac{100}{1 + \exp(a\mathrm{FL} + b)},$$

where a and b are fitted parameters and $L_{50} = -b/a$. We also calculated the percentage of maximum length (MAXLEN) at which sexual maturity occurred. This ratio has been used to compare proportionate size at maturity for species by habitat type, zoographic province, or depth range (Grimes 1987).

Sex ratios were compiled and examined for significant deviation from unity and to determine whether sex ratio and size (in 50 mm FL intervals) were independent using chi-square statistics. Two-way contingency table analysis was performed to determine whether the sex ratio differed during the year when pooled into bimonthly periods.

RESULTS

Spawning Season

Spawning season was determined from a wide size range of uku and onaga (Fig. 1). The Spearman rank correlation coefficients (r_s) calculated by comparing GSI with stages I–III were $r_s = 0.6205$ for uku ($P < 0.0001$), and $r_s = 0.8685$ for onaga ($P < 0.0001$), indicating a positive relationship between GSI and stage of development for both species, although the correlation was considerably lower for uku. In addition, the range in GSI values representing stages II and III ovaries was greater for uku than for onaga (Fig. 2). Thus, rather than using GSI as the single method for estimating spawning seasonality by month or fish length, visual staging methods also were used.

Both species reached maturity in the spring and summer and spawned continuously until fall or early winter. Neither species reached stage II of development (vitellogenesis) at any other time of the year. Uku spawning began in May and peaked 1 month later in June, as evidenced by the sharp rise in GSI values and the presence of mature and ripe fish during this time (Figs. 3, 4).

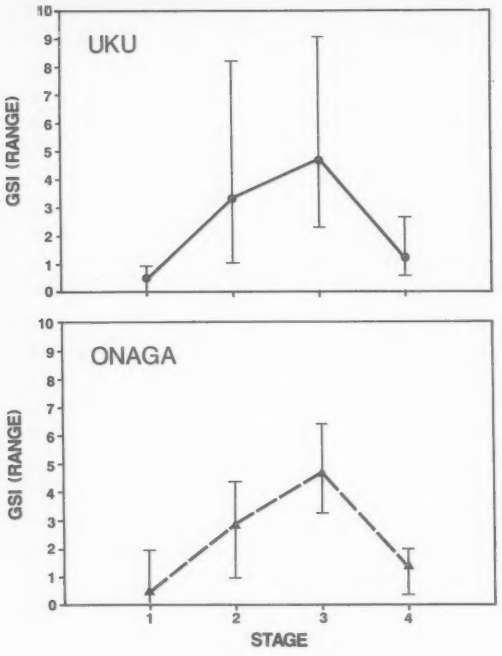


FIGURE 2.—Range in (A) uku and (B) onaga gonosomatic index (GSI) for each developmental stage designation in Table 1.

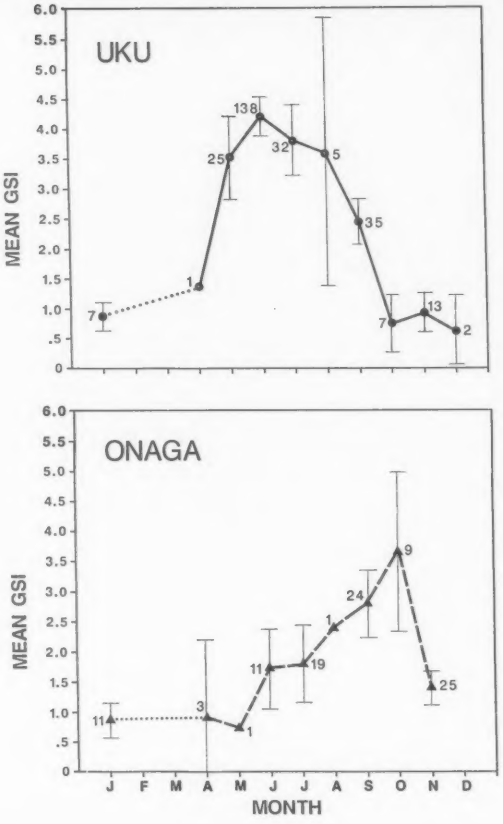


FIGURE 3.—Monthly mean gonosomatic index (GSI) for female uku and onaga. Bars indicate 95% confidence limits. Juvenile (<500 mm FL) uku and juvenile (<600 mm FL) onaga were excluded from analysis. Sample size is indicated next to each data point.

From July to October, the mean GSI values gradually decreased as spawning activity tapered off. By November, all fish examined were either partially or completely spawned (stage IV). Stage IV fish were not found during the spawning season.

In contrast, female onaga began maturing in June. Fully ripe onaga were not found until July, and spawning activity did not peak until October (Figs. 3, 4). The GSI values dropped sharply in November as the incidence of completely spawned and partially spawned individuals abruptly increased. As with uku, completely spawned individuals were not found until the close of the spawning season. Mean monthly GSI values for male onaga reflected a similar pattern.

Size at Sexual Maturity

Uku matured at a substantially smaller size than onaga. Fifty percent of the female uku attained sexual maturity at 425–475 mm FL, as evidenced by elevated GSI's (Fig. 5) and by the percentage of fish judged mature by visual staging (Table 2). By the time the fish reached the

TABLE 2.—Stage of maturity, compared by 50 mm fork length (FL) size classes, for uku and onaga sampled during their respective spawning seasons.

Uku			Onaga		
FL (mm)	*N*	Percentage mature	FL (mm)	*N*	Percentage mature
275–324	2	0	475–524	11	9
325–374	1	0	525–574	15	7
375–424	2	0	575–624	12	33
425–474	3	66	625–674	4	25
475–524	12	100	675–724	13	77
525–574	21	100	725–774	13	92
575–624	18	95	775–824	16	100
625–674	20	95	825–874	6	100
675–724	15	94	875–925	5	100
725–774	4	100			
775–824	5	100			

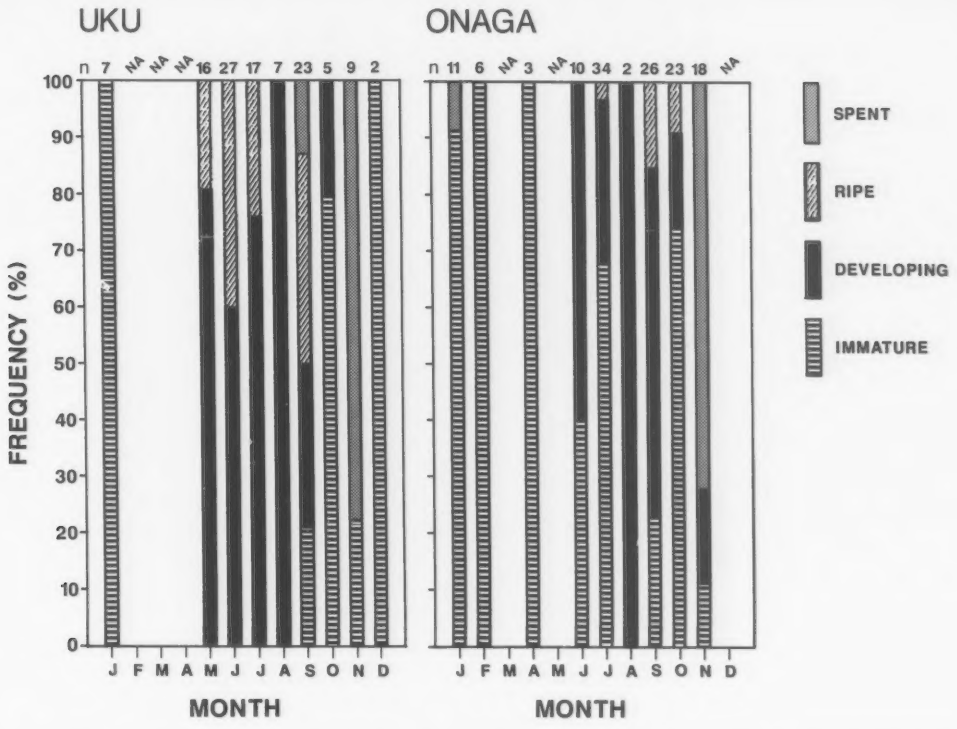


FIGURE 4.—Monthly percentages of uku and onaga ovaries at various stages of development determined by visual staging methods. N = number of samples per month.

500 mm size class, 100% were mature. The smallest uku with vitellogenic (stage II) ovaries during the spawning season was 429 mm FL (1.27 kg), which is 41.7% of the maximum length (MAXLEN) recorded for the study animals. The smallest individual with ripe (stage III) ovaries was 477 mm FL (1.82 kg) or 46.4% of the MAXLEN. The predicted value of L_{50} obtained from the logistic fit of percentage mature on FL (Fig. 6) was 449 mm FL (a = −0.3444, b =

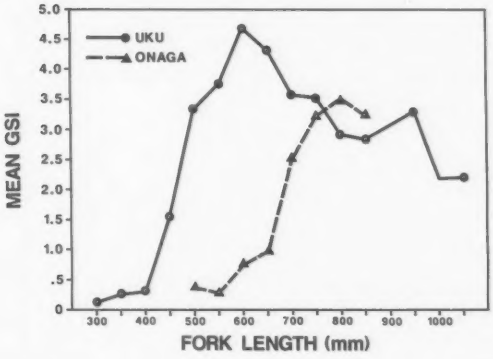


FIGURE 5.—Mean gonosomatic index (GSI) plotted by 50 mm FL intervals for female uku and onaga sampled during their respective spawning seasons.

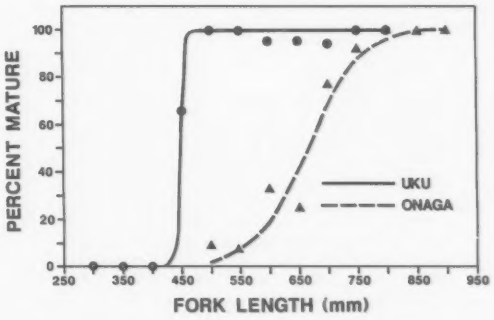


FIGURE 6.—Proportion of sexually mature female uku and onaga within each size class, plotted with the predicted proportion of mature females.

154.31). Interesting to note was the propensity for decreasing mean GSI's in uku larger than 600 mm FL (Fig. 5).

In contrast, the smallest mature onaga was 522 mm FL (2.22 kg) or 53.9% MAXLEN, and ripe individuals were not encountered until 605 mm FL (3.22 kg) or 62.4% MAXLEN. The predicted value of L_{50} obtained from the logistic fit of percentage mature on FL was 663 mm FL ($a = -0.0233$, $b = 15.462$; Fig. 6), and 77% of the onaga in the 675–725 mm FL class were found to be at stage II of development or beyond (Table 2). Onaga spawned over a narrower size range (600–900 mm FL; Fig. 5) compared with uku (450–1,050 mm FL; Fig. 5).

Histological examination of ovaries indicated that both species follow a similar pattern of development (Fig. 7). The progression from oogonia to hydration is typical of snappers and has been covered in detail by Crossland (1977) and Wallace and Selman (1981). Postovulatory follicles were not identifiable in tissue sections from ripe (stage III) ovaries of either species. None of the immature (stage I) ovaries examined histologically showed signs of atresia, indicating that these fish had not previously spawned. Identifiably atretic individuals in later stages of development were not observed until the end of the spawning season.

Spawning Frequency and Pattern of Egg Release

The size-frequency distributions of oocyte diameter were constructed for ovaries of uku caught during the spawning season, using the volumetric method, and were found to be polymodal, suggesting that uku may release multiple egg batches (Fig. 8a). All ovaries possessed a

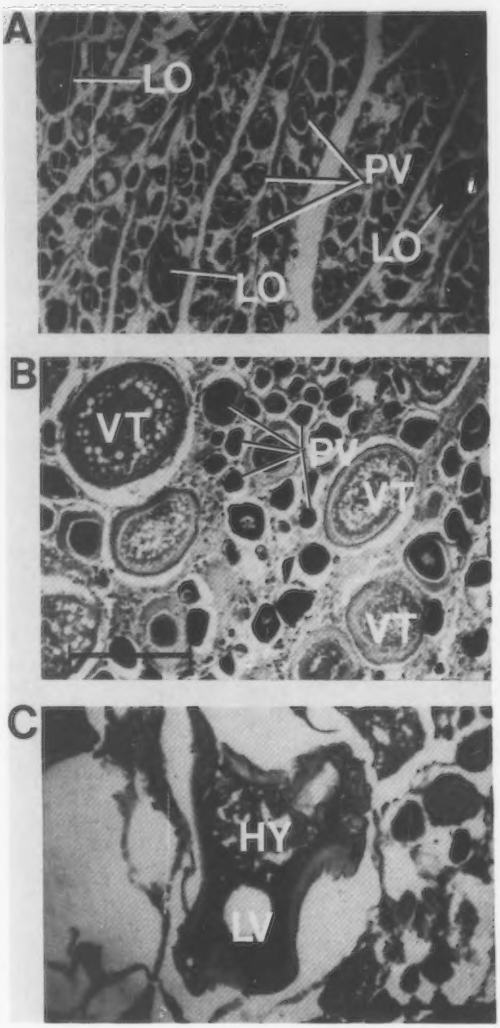
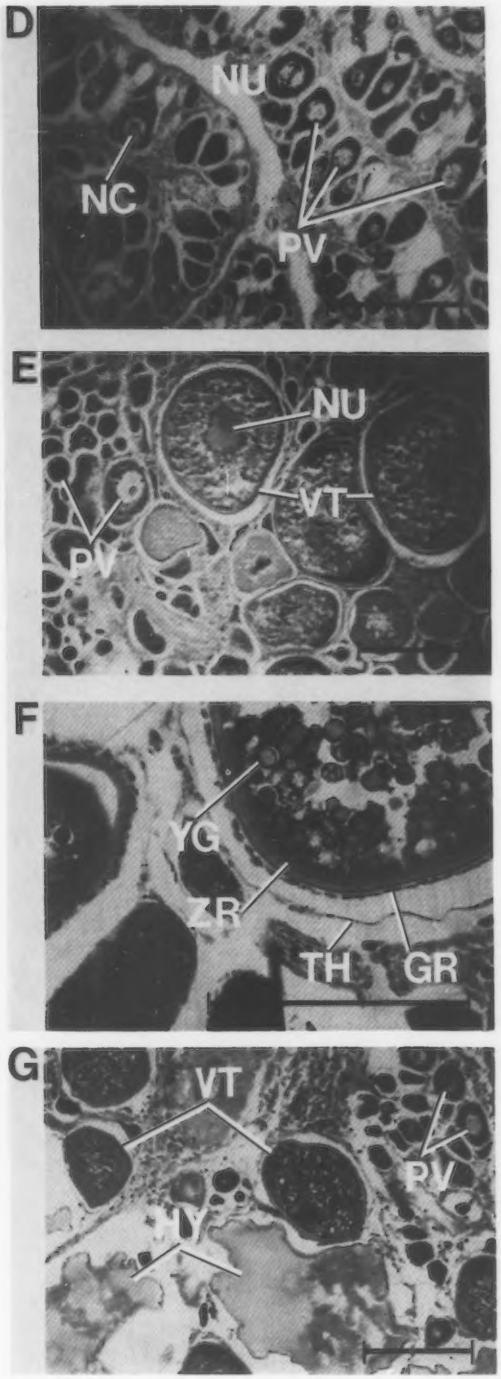


FIGURE 7.—Photomicrographs showing transverse histological sections of uku and onaga ovaries in various stages of development. Scale bars represent 0.10 mm. A. Early developing uku (386 mm FL) ovary classified as juvenile (stage I) containing numerous previtellogenic (PV) oocytes. Larger oocytes (LO) have reached the lipoid or yolk vesicle stage, just prior to vitellogenesis. B. Developing (stage II) uku (525 mm FL) ovary. Shown are previtellogenic (PV) and vitellogenic (VT) oocytes. C. Ripe (stage III) uku (541 mm FL) ovary with hydrated (HY) oocytes. Lipoid vesicles have fused to form a single mass (LV). D. Juvenile (stage I) onaga (506 mm FL) ovary consisting of previtellogenic (PV) oocytes with large central nucleus (NU) containing numerous nucleoli (NC). E. Developing (stage II) onaga (753 mm FL) ovary showing numerous mature oocytes in different stages of vitellogenesis (VT). F. Enlargement of a developing onaga ovary. Shown are granulosa (GR) and thecal (TH) cell layers, zona radiata (ZR), and yolk granules (YG). G. Ripe (stage III) onaga (605 mm FL) ovary showing hydrated (HY), vitellogenic (VT) and previtellogenic (PV) oocytes.



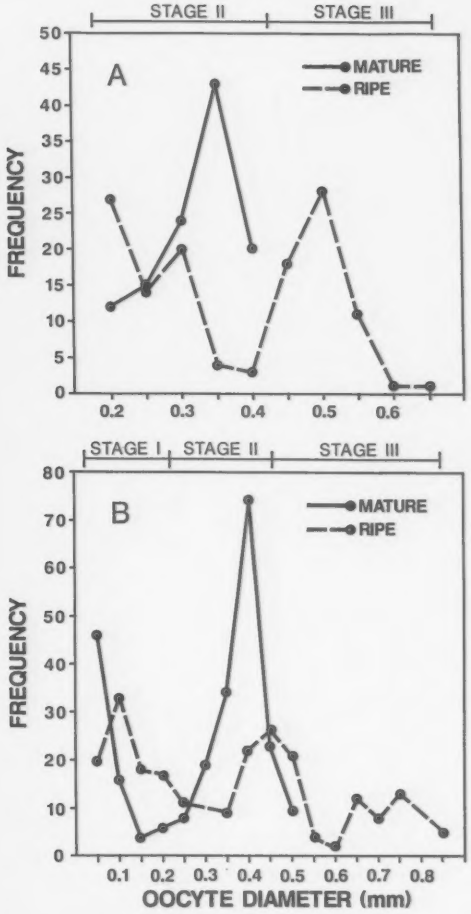


FIGURE 8.—Size-frequency distributions of uku ovaries in various stages of development (cf. Table 1) preserved in (A) Gilson's fluid and (B) Bouin's fluid. Each distribution shown represents a single ovary.

mode of immature oocytes not represented in the figure. Stage II ovaries contained a mode of oocytes at 0.30–0.35 mm, representing various stages of vitellogenesis, while stage III ovaries included this developing mode and another mode (0.50 mm) nearing hydration. A large amount of variation was noted in the relative frequency of oocytes in the most advanced mode of the stage III ovaries. Similar results were exhibited for size-frequency distributions of uku ovaries constructed by the cork borer method. This method allowed delineation of the immature mode as well as the other advanced stages (Fig. 8b). Additional evidence that multiple batches of

oocytes ripen and are successively spawned was indicated by the wide range in GSI values calculated for both species during the spawning season.

Sex Ratio

The sex ratio of male to female uku was 1.05:1 (51.2% males, $N = 559$ individuals combined). A chi-square goodness of fit test suggested that this ratio was not significantly different from the expected 1:1 ratio ($\chi^2 = 0.302$, $P > 0.05$). By examining sex ratio at 50 mm FL intervals, independence was determined and the percentage of females was shown to decrease between the 600 and 750 mm FL categories from 50.0 to 40.9%, then increase 65.5% at 800 mm FL before reaching 100% beyond 900 mm FL. Based on two-way contingency table analysis, the percentage of females caught increased significantly towards the end of the spawning season (September–October; Table 3). Males were caught in higher percentages in the spawning months from May to July.

DISCUSSION

The spawning season for both uku and onaga extends throughout the summer months in Hawaii, as evidenced by the advanced condition of the ovaries and the peaks in ova diameters and GSI values during this period. This pattern has been reported in Hawaii for other snapper species, including *E. carbunculus* (Everson 1984) and *P. filamentosus* (Kikkawa 1984). Spawning activity also occurs during the austral summer for populations of *A. virescens* from New Caledonia (Fourmanoir and Laboute 1976) and East Africa (Talbot 1960; Nzioka 1979). Likewise, peak summer spawning with intermittent activity throughout the rest of the year seemed to be the pattern for *E. coruscans* in Vanuatu (Brouard and Grandperrin 1985). The seasonal peak in spawning activity may be most closely tied to increases in water temperature and day length, as suggested by Walsh (1987) who observed that spawning activity for Hawaiian reef fishes declined rapidly in September to October as maximum water temperatures were reached.

TABLE 3.—Tests of the hypothesis that sex ratio of uku and onaga did not vary significantly from the sample populations during the year. Data are pooled by 2 mo intervals for samples collected in 1984–87 (df = 5).

	Uku			Onaga		
Month	*N*	Percentage female	Contribution to total χ^2	*N*	Percentage female	Contribution to total χ^2
Jan.–Feb.	15 } 17			56	37.5	0.277
Mar.–Apr.	2 }	47.0	0.027	19	15.8	4.976
May–June	359	46.5	0.776	23	60.9	3.771
July–Aug.	88	43.0	1.637	76	47.4	1.292
Sept.–Oct.	69	63.8	6.153	130	33.9	2.719
Nov.–Dec.	28	64.3	2.673	62	41.9	0.174
Total			11.266*			13.209*

* = $P < 0.05$.

The sex ratio of male to female onaga differed significantly ($\chi^2 = 8.99$, $P < 0.05$) from 1:1 in favor of males (61.4%, $N = 347$ individuals combined). The overall ratio of males to females was 1.59:1. There was a significant preponderance of males within the 50 mm FL intervals from 600 to 750 mm. However, females predominated above 850 mm FL, reaching 100% of the individuals in the 950 mm FL category. The two-way contingency table analysis suggested that sex and month of capture were not independent (Table 3).

This pattern would ensure optimum temperature conditions for developing larvae. A similar post-summer spawning decline associated with changing local environmental conditions was noted by Grimes and Huntsman (1980) for *Rhomboplites aurorubens* from North and South Carolina and by Everson (1984) for *E. carbunculus*. The extension of onaga's spawning season into November, with a peak in October, may reflect that the genus *Etelis* is restricted to much greater depths than are the other reef-associated lutjanid species. Seasonal changes in

temperature and photoperiod are much less pronounced at these depths. In Vanuatu, Brouard and Grandperrin (1985) found that seasonal changes in gonad maturation based on GSI values differed among species inhabiting discrete depths.

Grimes (1987) has suggested two distinct spawning patterns for snappers. One is a restricted pattern with spawning centered around the summer months, typical of species associated with continental habitats where peaks in production cycles occur because of nutrient run-off resulting from high rainfall. The opposing pattern is characterized by year-round spawning with peaks occurring in spring and fall, a pattern thought to be typical of less productive insular populations. Grimes (1987) has noted that Cuba and New Caledonia are large islands that follow the continental pattern, with spawning peaks arising during periods of high rainfall. *Etelis carbunculus* (Everson 1984) and *P. filamentosus* (Kikkawa 1984) have also been reported to follow a restricted spawning pattern in the Northwestern Hawaiian Islands. Both uku and onaga in our study also followed the restricted spawning pattern associated with continental habitats. Spawning took place over a protracted period centered around the summer months. Neither species was found in spawning condition at any other time of the year. Since temporal primary production cycles exhibit little seasonal variation throughout the Hawaiian Archipelago (Bienfang and Szyper 1981; Bienfang et al. 1984), the basis for this restricted pattern observed for uku and onaga is unclear. Apparently, the seasonal changes in day length and water temperature in Hawaii provide adequate spawning stimuli.

Interspecies differences in size at sexual maturity also were noted. The slope of the logistic curve fitted to the size at sexual maturity data was considerably steeper for uku compared with onaga (Fig. 6). Uku matured at 450–500 mm FL, with nearly 100% mature above 550 mm FL, and onaga matured at 550–800 mm FL, with 100% mature at 850 mm FL. Size at sexual maturity differed between species in terms of the percentage of MAXLEN at which maturity occurred. Uku began maturing at about 429 mm FL or 42% of their MAXLEN, whereas onaga began maturing at about 522 mm FL or 54% of their MAXLEN. Talbot (1960) reported that male and female *A. virescens* of East Africa reached maturity at 410 mm SL (51%) and 465 mm SL (58%), respectively. *Aprion virescens* off Vanuatu matured at 440 mm FL, a figure that Brouard and Grandperrin (1985) calculated from a MAXLEN coefficient of 57.6%, which was based upon the average values obtained from 34 tropical fish species from the west coast of Africa. The same coefficient, applied to Vanuatu populations of *E. coruscans*, indicated that sexual maturity was reached at 470 mm FL, although developmental staging data obtained for this species revealed that mature fish were first sampled at 330–380 mm FL. The actual size at which maturity commenced in all of these locations agreed closely with our data for uku in Hawaii, while the percentage of MAXLEN values differed considerably. However, Hawaii and Vanuatu populations of onaga matured at substantially different sizes.

Disparities in size at sexual maturity between areas may reflect differences in resource utilization and growth allocation. Grimes (1987) calculated the average percentage of MAXLEN at which sexual maturity occurred for lutjanid populations occupying similar zoogeographic locations and habitats. Insular and continental populations had average MAXLEN values of 51 and 43%, respectively, while the deep (> 91 m) and shallow (< 91 m) species were calculated at 49 and 43%. The MAXLEN value of 42% calculated for the study population of uku indicates that this species fits the shallow, continental pattern. As previously mentioned, onaga are found at much greater depths and therefore seem to be less influenced by continental effects than uku. These observations are substantiated by the fact that the MAXLEN value of 54% calculated for onaga conforms closest to the deep, insular pattern reported in Grimes (1987). He reasoned that these anomalies may result from regional differences in food production. Fish from a relatively resource-rich environment may mature at a proportionally smaller size than fish in less productive habitats. He further speculated that selection may favor maturation at a larger maturing size in insular regions because the cost of year-round spawning may be higher in these areas.

Estimates of von Bertalanffy growth parameters, derived from weight-frequency distributions for uku and onaga landed in Hawaii in 1984–86, indicate that uku mature at about ages 4–5 (429 mm FL), while onaga begin maturing at ages 5–6 (522 mm FL) (Ralston and Kawamoto, fn. 1). In the same study, Ralston and Kawamoto (fn. 1) calculated the size at entry to the fishery

as 650 mm FL for uku and 450 mm FL for onaga in the main Hawaiian Islands, indicating that, for onaga, the present fishery is capturing individuals that have not yet reached sexual maturity. Continuing this practice could lead to a serious decline in spawning stock biomass (Polovina 1987).

Sex ratio also differed between the two species. The ratio of male to female uku was judged not significantly different from the expected ratio of 1:1. In contrast, the onaga sex ratio was significantly different from unity in favor of males. Females dominated in the larger size classes for both species. The preponderance of large females has also been reported for other snapper species, including *Lutjanus synagris* (Reshetnikov and Claro 1976), *R. aurorubens* (Grimes and Huntsman 1980), and *E. carbunculus* (Everson 1984). This phenomenon is thought to be due to differential mortality of the sexes rather than to growth (Wenner 1972; Grimes and Huntsman 1980). The preponderance of male onaga in the smaller size ranges is more difficult to explain and may reflect intersexual behavioral differences. If smaller males feed more aggressively, they would be overly abundant in the catch. Differences in feeding behavior may also explain monthly variations in sex ratio reported for both species. The ratio of female uku increased markedly at the close of the spawning season, suggesting a heightened vulnerability to the fishing gear owing to what may be greater nutritional demands of postspawning females. Seasonally, the largest catch of uku occurs in summer (May–October), when fish are thought to form spawning aggregations (Ralston, fn. 2).

Numerous investigators have suggested that snappers are multiple spawners, based upon the presence of multiple size modes of developing oocytes (Min et al. 1977; Grimes and Huntsman 1980; Everson 1984; Kikkawa 1984; Grimes 1987). Other evidence reported as substantiating this phenomenon has been the wide variations exhibited in GSI's of *L. griseus* (Starck and Schroeder 1970) and *R. aurorubens* (Grimes and Huntsman 1980) during the spawning season. Ralston (1981) suggested that *P. filamentosus* is a multiple spawner because the ovaries of ripe females make up only about 4% of the total body weight, a relatively small percentage compared with that of a single spawning temperate species. These observations, the presence of multiple size modes of developing oocytes and the wide variations in GSI's, were noted for uku and onaga and suggested that these species also spawn repeatedly during the spawning season. Although it has been documented that the oocyte size-frequency distribution of many snapper species contains two or three distinct modes, the exact number of batches spawned per season is rarely reported. This is because the process of recruitment from the undifferentiated oocyte pool is dynamic and difficult to characterize (Grimes 1987).

Much of the above evidence is largely contingent on the assumption that multiple oocyte modes continue to develop and are successively spawned. Foucher and Beamish (1980) observed that, for Pacific hake, *Merluccius productus*, from the Strait of Georgia, oocyte development was multimodal during the spawning season, suggesting multiple spawning for this species. Histological examination of the ovaries revealed, however, that only the largest batch became hydrated and was spawned and all remaining residual yolked oocytes were resorbed. More direct evidence for this mode of spawning, as well as the delineation of the number of batches spawned, has been obtained through the process of identifying and ageing postovulatory follicles in species that exhibit these multiple modes of oocyte development. This method has been used to estimate spawning frequency in several engraulid species (Hunter and Goldberg 1980; Hunter and Macewicz 1980, 1985; Alheit et al. 1984; Parrish et al. 1986; Clarke 1987) and also for the skipjack tuna, *Katsuwonus pelamis* (Hunter et al. 1986). Ageing postovulatory follicles seems to work well for species normally found in large aggregations or schools but has yet to be applied to snappers. The ageing method using postovulatory follicles may be more difficult to apply to such species as snappers, which are known to occur in fewer numbers. Although our study attempted to identify postovulatory follicles in natural populations of uku and onaga, they could not be positively identified or aged. Future studies will have to address this problem, since the delineation of spawning frequency is important for accurate fecundity estimates.

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Larval Development of the Australian Devilfish, *Gymnapistes marmoratus* (Teleostei: Scorpaenidae)

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ABSTRACT: The larval development of the devilfish, *Gymnapistes marmoratus*, is described from material collected in the Swan and Peel-Harvey Estuaries in southwestern Australia. Larvae of *G. marmoratus* examined (2.6–9.3 mm BL) are pelagic and characterized by a deep and compressed, lightly pigmented body; a moderately short gut; 29 myomeres; complex head spination; and large, pigmented fan-shaped pectoral fins which form early in development. Notochord flexion occurs between 4.8 and 6.0 mm BL and transformation between 6.8 and 10.9 mm BL.

The majority of head spines in *G. marmoratus* form before the postflexion stage. These include parietal, supraocular, preopercular, nasal, pterotic, posttemporal, and some suborbital spines. The suborbital stay develops after flexion; the nuchal and three of the anterior preopercular spines disappear in juveniles. The caudal complex of larval *G. marmoratus* includes well-fused hypural elements 1 and 2 and hypural elements 3 and 4, a reduced fifth hypural bone, and a parhypural element.

In addition to larval development, comparisons with similar taxa and the occurrence of the larvae in the Swan Estuary are discussed.

Scorpaeniform fishes are represented in southwestern Australia by one marine species of each of *Centropogon*, *Scorpaena*, *Maxillicosta*, *Gymnapistes*, and *Glyptauchen* and three of *Neosebastes* (Hutchins and Thompson 1983; Hutchins and Swainston 1986). The larval stages of none of these genera have been described except for those of *Scorpaena*, which were described from larvae caught elsewhere (see Moser et al. 1977; Washington et al. 1984a). The present paper describes for the first time the larval development of the sole species of the genus *Gymnapistes*, *G. marmoratus*, using material collected in the Swan and Peel-Harvey Estuaries in southwestern Australia. This paper also includes information on the occurrence and distribution of the larvae in the Swan Estuary.

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The devilfish, *Gymnapistes marmoratus*, also known as the soldier fish or South Australian cobbler, is a marine species common in seagrass beds of coastal embayments and estuaries of southern Australia. It occurs between southern Sydney in New South Wales and Fremantle in Western Australia and occurs also in Tasmania (Hutchins and Thompson 1983; Last et al. 1983; Hutchins and Swainston 1986). Juveniles are relatively common in both the lower Swan Estuary and the Peel Inlet, in southwestern Australia (Chubb et al. 1979; Potter et al. 1983).

The population of *G. marmoratus* studied by Grant (1972) in the D'Entrecasteaux Channel, southern Tasmania, spawned at the beginning of spring at approximately two years of age. In the Gippsland Lakes, Victoria, the adults apparently spawn over an extended period with a peak in winter (Ramm 1986). Larvae of this species have been collected from July to October in Port Phillip Bay, Victoria, with peak abundance occurring in August (Jenkins 1986).

MATERIALS AND METHODS

Collection of Larvae

Larvae of *G. marmoratus* were obtained from plankton samples collected monthly during 1986 in the lower Swan Estuary (lat. 32°04′S, long. 115°44′E). Samples were obtained at night using 0.6 m diameter paired bongo nets, with 0.5 mm mesh, which were towed horizontally 0.5 m below the surface for 10 minutes. Transforming and juvenile *G. marmoratus* were caught in the Peel-Harvey Estuary (32°35′S, 115°45′E) using a 3.0 mm mesh beach seine. Samples were fixed in 10% formalin and specimens were stored in 70% alcohol.

Material Examined

A total of 22 larvae, ranging in body length (BL) from 2.6 to 6.8 mm, were used to describe pigmentation, morphometrics, and meristics. One transforming larva (9.3 mm BL) and seven

benthic juveniles, ranging from 10.9 to 16.8 mm BL, were also examined. Ten representative larval *G. marmoratus* were deposited in the Western Australian Museum (Perth) under the catalogue number P-29814-001.

Measurements and Counts

Larval and juvenile *G. marmoratus* were measured to the nearest 0.1 mm using a Wild M8[1] dissecting microscope fitted with an ocular micrometer. Terminology and body measurements of larvae follow Leis and Rennis (1983). All lengths except body length (BL, mm), i.e., the notochord length in preflexion and flexion larvae and the standard length in postflexion larvae, are expressed as a percentage of body length. Myomere counts and fin ray counts of paired fins were made on the left side of the body. Pigment refers to melanin. Illustrations were done with the aid of a drawing tube.

Six larval, one transforming, and three juvenile *G. marmoratus* were cleared and double stained for bone and cartilage following the technique of Potthoff (1984), as modified from Dingerkus and Uhler (1977). These specimens were used to count fin rays and vertebrae, to determine the sequence of bone ossification, and to describe the development of both the head spines and the caudal complex. The term "ossified" refers solely to structures stained positively for bone. The terminology used for describing the head spination and the caudal complex was modified from that of Washington et al. (1984a) and Feeney (1986) respectively.

RESULTS

Identification

Larvae were identified as scorpaenids by the well-developed head spination, the continuous dorsal fin, and the large, fan-shaped, pigmented pectoral fins (Leis and Rennis 1983). Specimens were initially assembled in a series according to the degree of formation of the pectoral fins which, when fully formed, have 11 fin rays. Large specimens were identified as *G. marmoratus* by dorsal and anal fin ray counts of XIII, 9 and III, 6 respectively and the elongate infraorbital spine (Scott et al. 1980; Last et al. 1983). Fin ray counts, head spination, and body pigment were used to link larvae and juveniles.

Description of Larvae

Larvae of *G. marmoratus* are pelagic prior to transformation. Larvae are initially elongated, becoming deep-bodied (12–36% BL) and laterally compressed with development (Table 1, Figs. 1, 2). The smallest larva illustrated (3.3 mm, Fig. 1A) possesses pectoral fin buds and a dermal sac enclosing most of the body but has neither head spines nor traces of yolk sac. The head length increases from 13% BL in preflexion larvae to 38% BL in postflexion larvae (Table 1). The mouth is formed by 3.3 mm and teeth appear along the premaxilla and dentary at 6.8 mm. The gut is coiled and short in small larvae. The preanal length increases from 35% BL in preflexion larvae to 61% BL in postflexion larvae (Table 1, Figs. 1, 2). There is a moderate gap between the anus and the origin of the anal fin in postflexion larvae (Fig. 2). A prominent swimbladder becomes visible above the gut from about 3.3 mm, but it is no longer externally visible by 10 mm.

Larval *G. marmoratus* possess 29 myomeres. Double-stained specimens have 28 vertebrae (Table 2). Notochord flexion commences by 4.8 mm and is complete by 6.0 mm. Transformation from the pelagic larva to the benthic juvenile occurs between 6.8 and 10.9 mm (Fig. 2A, B).

Fin Development

The development of fins in larval and juvenile *G. marmoratus* is summarized in Table 2. Pectoral fins develop very rapidly, attaining a length of 44% BL in postflexion larvae (Table 1, Fig. 2A). Incipient fin rays of the pectoral fin are visible by 3.3 mm, and all 11 fin rays are formed by 4.7 mm. The caudal fin starts to form by 4.6 mm and is completely developed shortly after notochord flexion is complete (Figs. 2A, 4C). The dorsal and anal fin anlagen appear by 5.0 mm, i.e., prior to completion of notochord flexion, and the rays start to form sequentially from tail to head. Rays and spines, both dorsal (XIII, 9) and anal (III, 6), are developed by 9.0 mm (Table 2). Pelvic buds are visible by 4.8 mm and fin rays are formed by 9.3 mm.

Pigmentation

Larval *G. marmoratus* are lightly pigmented prior to transformation. In preflexion larvae, the

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Morphometric measurements for larval, transforming, and juvenile *Gymnapistes marmoratus*. Body intervals are expressed as a percentage of body length; *n* = number of individuals. Means and standard deviations (in parentheses) are given when $n > 1$. Blanks indicate character is absent. Individuals indicated with * and ** correspond to a transformed larva and juveniles respectively. Individuals between dashed lines were undergoing notochord flexion.

Body length (mm)	*n*	Head length	Snout length	Eye diameter	Body depth at pectoral fin base	Pectoral fin length	Preanal length	Predorsal fin length
2.6	1	17.7	3.4	7.6	12.7	7.6	38.4	.
2.7	1	13.7	2.8	7.9	14.4	15.2	36.1	.
3.3	1	17.8	2.9	7.5	17.8	19.0	38.7	.
4.0	1	19.6	4.6	7.6	16.6	20.6	40.2	.
4.6	1	19.6	3.8	7.2	15.0	27.8	35.2	.
4.7	1	22.4	4.7	7.1	17.5	31.2	41.6	.
4.8	1	23.9	5.7	7.8	23.5	32.9	45.7	.
5.0	1	25.2	4.3	8.3	25.0	35.6	47.0	54.8
5.1	2	23.4(0.10)	5.7(0.50)	7.6(0.05)	21.4(1.25)	35.2(0.15)	45.4(2.50)	58.6($n = 1$)
5.2	1	24.3	6.0	7.1	21.0	33.7	45.5	.
5.3	1	23.9	5.4	8.1	22.0	33.1	49.3	56.1
5.5	1	30.4	7.5	8.5	24.3	34.0	49.6	59.6
5.7	1	29.2	6.5	8.7	24.6	38.0	54.5	58.5
5.8	1	32.0	8.8	8.4	27.6	42.4	50.7	28.9
5.9	1	27.6	5.3	8.7	24.9	35.7	51.6	57.2
6.0	2	30.0(0.49)	7.9(0.75)	7.5(0.00)	24.9(1.33)	34.6(0.08)	51.6(1.08)	59.8(0.00)
6.1	1	32.4	7.0	8.5	26.6	35.7	57.8	32.1
6.2	2	29.6(2.45)	7.5(0.75)	8.1(0.10)	27.6(0.95)	34.6(0.60)	54.7(1.45)	28.8(0.95)
6.8	1	32.6	9.0	8.4	27.7	43.9	57.2	30.6
9.3*	1	33.3	7.4	9.8	30.5	31.2	62.8	29.0
10.9**	1	34.0	6.8	9.9	32.3	27.1	63.1	27.8
13.9**	1	35.6	6.9	10.2	33.9	30.3	60.4	24.5
14.1**	1	36.0	8.7	9.2	33.8	32.6	64.1	30.3
15.1**	1	37.6	6.3	10.9	35.7	34.7	60.3	23.9
15.7**	1	36.6	6.7	10.3	31.8	29.2	60.5	23.2
15.8**	1	36.7	8.2	9.7	36.7	29.8	61.6	23.1
16.8**	1	38.6	7.5	10.1	31.9	30.1	61.3	21.7

head has one melanophore at the angle of the lower jaw, one ventral melanophore at the gular area, and a group of internal melanophores at the base of the hindbrain. All of these melanophores are retained (Figs. 1, 2). Melanophores appear on the midbrain by 4.9 mm and develop over the snout, opercular, and gular areas by 6.0 mm.

The dorsal surface of the swimbladder and ventral surface of the gut are pigmented in preflexion larvae. A single row of melanophores occurring along the ventral surface of the gut in small larvae persists throughout development (Figs. 1, 2). Melanophores appear externally on the lateral surface of the trunk by 6.2 mm and expand over the gut area by 9.5 mm (Fig. 2A, B). A single row of 16–22 melanophores is present on the ventral surface of the tail in preflexion larvae, each melanophore spaced about one per myomere. This single row of melanophores becomes double along the anal fin base in postflexion larvae. Pigment appears on the dorsal surface of the body by 5.5 mm and, shortly after, on the lateral surface of the body. Transition from larval to juvenile pigmentation begins by 6.8 mm. Juveniles develop blotches of pigment on the head, trunk, and dorsal and anal fin membranes (Fig. 2B).

Melanophores appear on the pectoral fins by 3.3 mm (Fig. 1A), extend distally on each pectoral ray by 4.6 mm, and remain along the edges of the distal portion of the rays throughout development (Fig. 2A). In larvae over 10 mm, patches of pigment form on the pectoral fin bases and on the fin membranes (Fig. 2B). Melanophores appear on the dorsal and anal fin membranes by 6.0 mm, and patches of pigment form on the membranes of these fins by 10 mm. The

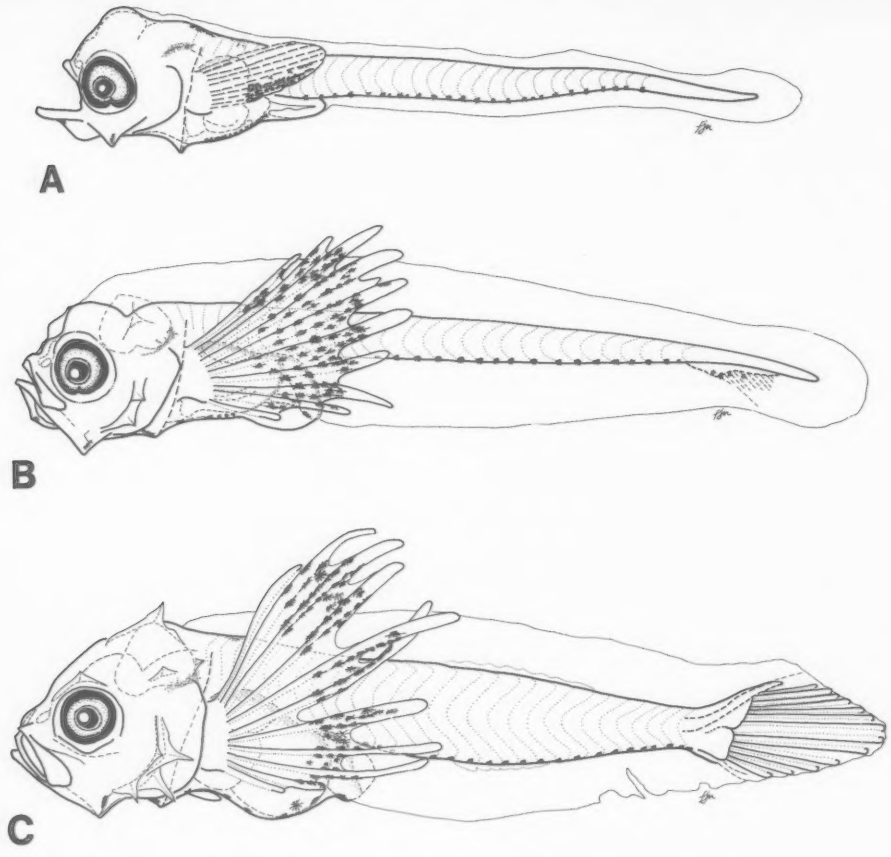

FIGURE 1.—Larvae of the devilfish, *Gymnapistes marmoratus*, caught in the lower Swan Estuary in July 1986. (A) 3.3 mm BL larva. (B) 4.6 mm BL larva. (C) 5.1 mm BL larva; note pelvic fin buds.

TABLE 2.—Fin ray development and vertebral counts in larval, transforming, and juvenile *Gymnapistes marmoratus*. Vertebrae were counted only in cleared and double-stained specimens (denoted by *) in which vertebrae were clearly differentiated. Other blanks indicate character is absent. Pectoral and pelvic fin ray counts were made on the left side of the body. Procurrent fin rays are shown as dorsal/ventral elements.

Body length (mm)	*n*	Stage	Dorsal fin	Anal fin	Pectoral fin	Pelvic fin	Caudal fin rays	Procurrent rays	Vertebrae
2.6	1	Preflexion			bud				
2.7	1	Preflexion			bud				
3.3	1	Preflexion			8				
4.0*	1	Preflexion			10				
4.6	1	Preflexion			10				
4.7*	1	Preflexion			11		9		
4.8	1	Flexion			11	bud	10		
5.0*	1	Flexion	anlage	anlage	11	bud	5+5		28
5.1	2	Flexion	anlage	anlage	11	bud	7+5		
5.2*	1	Flexion	anlage	anlage	11	bud	5+5		28

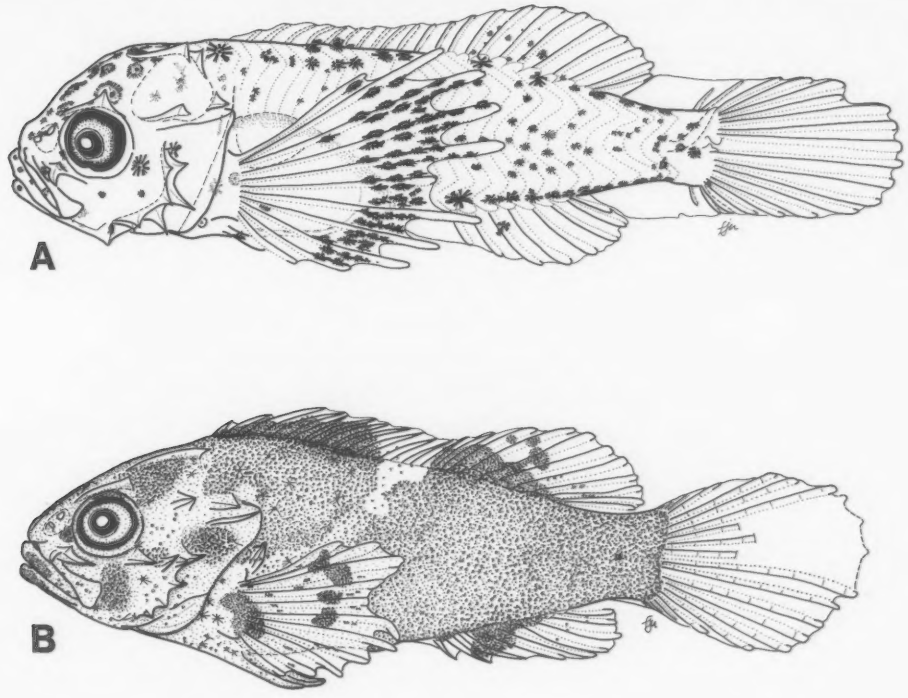

FIGURE 2.—Larva and juvenile of the devilfish, *Gymnapistes marmoratus*. (A) 6.2 mm BL larva collected in the Swan Estuary in July 1986. (B) 10.9 mm BL juvenile collected in the Peel-Harvey Estuary in August 1985; dashed lines indicate damaged caudal fin.

TABLE 2.—*Continued.*

Body length (mm)	*n*	Stage	Dorsal fin	Anal fin	Pectoral fin	Pelvic fin	Caudal fin rays	Procurrent rays	Vertebrae
5.3*	1	Flexion	8	6	11	bud	6+7	1/0	28
5.5	1	Flexion	8	5	11	bud	7+6	1/0	
5.7	1	Flexion	9	7	11	bud	7+6	1/1	
5.8	1	Flexion	10	7	11	bud	7+6	1/1	
5.9	1	Flexion	9	7	11	bud	7+7	1/2	
6.0	2	Flexion	9–10	7–8	11	bud	7+6	1/2–1	
6.1	1	Postflexion	9	8	11	bud	7+7	2/3	
6.2	2	Postflexion	19–22	III,5	11	bud	7+6	1–2/3	
6.8*	1	Postflexion	21	III,6	11	bud	7+7	3/3	28
9.3*	1	Transforming	XIII,9	III,6	11	I,5	7+7	5/5	28
10.9	1	Juvenile	XIII,9	III,6	11	I,5	7+7	5/5	
13.9	1	Juvenile	XIII,9	III,5	11	I,5	7+7	6/6	
14.1*	1	Juvenile	XIII,9	III,6	11	I,5	7+7	6/5	28
15.1*	1	Juvenile	XIII,9	III,6	11	I,5	7+7	6/5	28
15.7	1	Juvenile	XIII,9	III,6	11	I,5	7+7	6/5	
15.8	1	Juvenile	XIII,9	III,6	11	I,5	7+7	6/6	
16.8*	1	Juvenile	XIII,9	III,6	11	I,5	7+7	7/6	28

caudal fin remains unpigmented throughout development.

Development of Head Spines

Larvae of *G. marmoratus* have complex and well developed head spination (Fig. 3). Two posterior preopercular spines (PPO_2 and PPO_3) appear simultaneously at 4.6 mm (Fig. 1B; see Figure 3 for abbreviations also). Two more posterior preopercular spines (PPO_1 and PPO_4) develop by 5.7 mm and a fifth (PPO_5) by 10 mm. The PPO_1 spine becomes enlarged in juveniles, reaching a relative length of ca. 12% BL (Fig. 3D). Two anterior preopercular spines (APO_2 and APO_3) form by 4.8 mm, followed by a third anterior preopercular spine (APO_1) by 5.4 mm. All spines of both the anterior and posterior preopercular margins merge by 6.8 mm and only the APO_1 spine, the enlarged PPO_1 spine, and the PPO_{2-5} spines remain in juveniles (Fig. 3D).

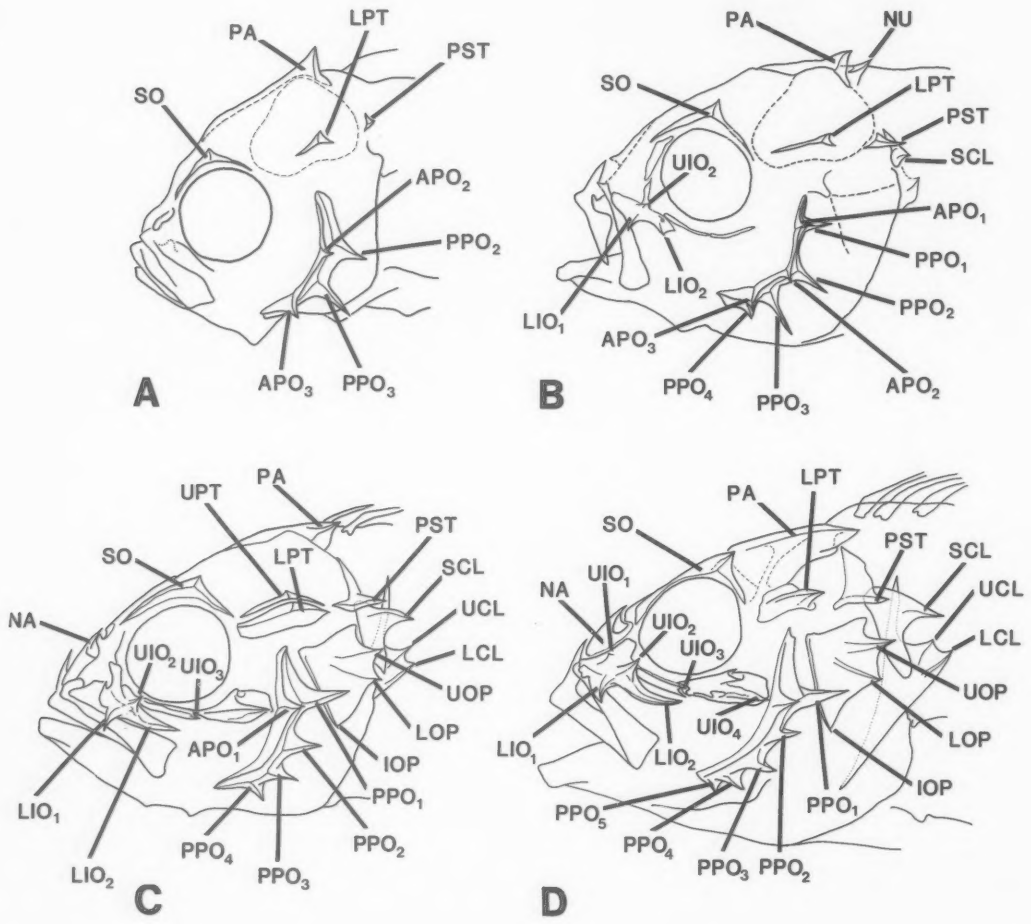

FIGURE 3.—Head spination in cleared and double-stained larval, transforming and juvenile *Gymnapistes marmoratus*. (A) 5.3 mm BL larva. (B) 6.8 mm BL larva. (C) 9.3 mm BL transforming larva. (D) 14.1 mm BL juvenile. Abbreviations: APO_1, 1st anterior preopercular; APO_2, 2nd anterior preopercular; APO_3, 3rd anterior preopercular; IOP, infraopercular; LCL, lower cleithral; LIO_1, 1st lower infraorbital; LIO_2, 2nd lower infraorbital; LOP, lower opercular; LPT, lower pterotic; NA, nasal; NU, nuchal; PA, parietal; PPO_1, 1st posterior preopercular; PPO_2, 2nd posterior preopercular; PPO_3, 3rd posterior preopercular; PPO_4, 4th posterior preopercular; PPO_5, 5th posterior preopercular; PST, posttemporal; SCL, supracleithral; SO, supraocular; UCL, upper cleithral; UIO_1, 1st upper infraorbital; UIO_2, 2nd upper infraorbital; UIO_3, 3rd upper infraorbital; UIO_4, 4th upper infraorbital; UOP, upper opercular; UPT, upper pterotic.

The parietal spines (PA) develop prior to flexion and are retained in juveniles but become blunt. The nuchal spines (NU) appear posterior to the parietal spines by 5.7 mm and disappear by 9.0 mm (Fig. 3C). The lower pterotic (LPT) and supraocular (SO) spines appear simultaneously at 4.8 mm and the posttemporal spine (PST) by 5.1 mm. A small upper pterotic spine (UPT) appears dorsal to the lower pterotic spine (LPT) by 9.0 mm and fuses to the LPT spine by 10.0 mm. All LPT, SO, and PST spines persist in juveniles (Figs. 2B, 3C, D).

The second upper infraorbital (UIO_2) and the first lower infraorbital (LIO_1) spines form simultaneously at 5.5 mm. The second lower infraorbital spine (LIO_2), which forms by 6.8 mm underneath the eye, grows backwards as a recurved hook reaching a relative length of ca. 16.5% BL in juveniles (Fig. 3B, C, D). The nasal (NA), upper and lower cleithral (UCL, LCL), and the upper opercular, lower opercular, and infraopercular (UOP, LOP, IOP) spines form during transformation and remain in juveniles (Fig. 3D).

Development of the Caudal Complex

The development of the caudal complex in larval *G. marmoratus* is illustrated in Figure 4. Three nonossified hypural elements (HY_1, HY_3, HY_4) form at about 4.7 mm ventral to the notochord (N) (Fig. 4A). The third and fourth hypural elements (HY_3, HY_4) fuse to form a plate by 5.3 mm (Fig. 4B), leaving a small fora-

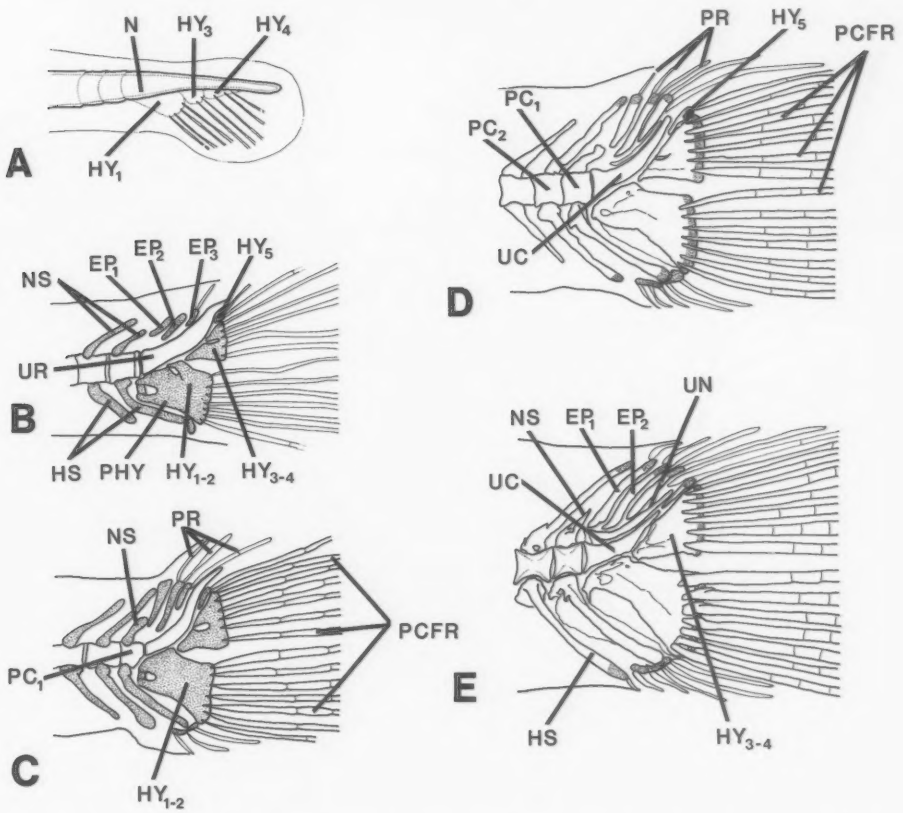

FIGURE 4.—Development of the caudal complex in cleared and double-stained larval, transforming, and juvenile *Gymnapistes marmoratus*. (A) 4.7 mm BL larva. (B) 5.3 mm BL larva. (C) 6.8 mm BL larva. (D) 9.3 mm BL transforming larva. (E) 14.1 mm BL juvenile. Shaded areas represent elements stained with alcian blue. Abbreviations: EP, epural; HS, haemal spine; HY, hypural; N, notochord; NS, neural spine; PC, preural centrum; PCFR, principal caudal fin ray; PHY, parhypural; PR, procurrent ray; UC, ural centrum; UN, uroneural; UR, urostyle.

men which disappears in juveniles (Fig. 4E). A fifth, reduced, hypural element (HY_5) forms ventral to the tip of the notochord by 5.3 mm and remains discrete from the upper hypural plate (HY_{3-4})in juveniles (Fig. 4B, E). Two distinct foramina are visible in the lower hypural plate (HY_{1-2}) by 5.3 mm. The distal foramen results from the fusion between HY_1 and HY_2 elements, whereas the proximal foramen is probably the result of the fusion between the lower plate (HY_{1-2}) and the parhypural element. Only the proximal foramen remains in juveniles (Fig. 4E). One principal caudal fin ray (PCFR) is attached to the uppermost hypural element (HY_5), six to the upper hypural plate (HY_{3-4}), and seven to the lower hypural plate (HY_{1-2}) by 6.8 mm. Both the HY_{1-2} and HY_{3-4} plates ossify by 9.0 mm and remain discrete from each other and from the ural centrum (UC) in juveniles (Fig. 4E).

Three epural elements (EP_1, EP_2, EP_3) appear dorsal to the urostyle (UR) at about 5.3 mm, with a single procurrent ray attached to the EP_3 (Fig. 4B). Ventral procurrent rays appear by 7.5 mm and the number increases to seven dorsal and six ventral procurrent rays by 16.8 mm (Table 2). A uroneural (UN) starts to form dorsal to the ural centrum by 9.0 mm, and it is completely formed by 14.0 mm (Fig. 4D, E). Nonossified neural (NS) and haemal (HS) spines form simultaneously shortly after flexion is commenced and all are ossified by 9.0 mm. The neural spine on the first preural centrum (PC_1) is reduced (Fig. 4, C, E).

DISCUSSION

Comparisons to Subfamilies of the Scorpaenidae

The larval development of *G. marmoratus* follows a similar pattern to that observed in other scorpaenid species (Washington et al. 1984a). The sequence of fin formation in larval *G. marmoratus* parallels that of larvae of the subfamilies Sebastinae and Scorpaeninae, except that the pelvic fins in *G. marmoratus* are completely formed following, rather than prior to, the formation of the anal and dorsal fins. Notochord flexion in larval *G. marmoratus* (4.8–6.0 mm) occurs at similar sizes to that observed in scorpaenine larvae (4.0–6.0 mm) but earlier than in sebastine (6.0–12.0 mm) and sebastolobine (6.0–7.3 mm) larvae (Washington et al. 1984a). In addition, transformation of *G. marmoratus* larvae occurs much earlier (6.8–10.9 mm) than in the larvae of the other three subfamilies (10.0–20.0 mm) (Washington et al. 1984a).

The majority of the head spines of *G. marmoratus* develop before the postflexion stage, as is the case in other scorpaenid larvae. The parietal spines are not as prominent as in sebastine and scorpaenine larvae and lack the serrations usually found in the parietal spines of the larvae of these subfamilies (Washington et al. 1984a). The small nuchal spines, which disappear in juveniles, are excluded from the parietal ridges and never exceed in length those of the parietal spines, as has been observed in other scorpaenine larvae. In addition, all anterior preopercular spines except the APO_1 spine disappear in larval *G. marmoratus* after flexion has been completed; the same spines disappear in sebastine larvae (Washington et al. 1984a). The prominent suborbital stay of larval *G. marmoratus* (LIO_2 spine), which starts to develop after flexion, is venomous in adult specimens (Hutchins and Thompson 1983; Last et al. 1983). In contrast to larval *G. marmoratus*, this suborbital spine is absent or incomplete in sebastine, scorpaenine, and sebastolobine larvae. The absence of a suborbital spine has been suggested as a plesiomorphic condition in Scorpaeniformes (Washington et al. 1984b).

The presence of well-fused hypurals 1 and 2 (lower hypural plate) and hypurals 3 and 4 (upper hypural plate) in the caudal complex of larval *G. marmoratus* represent a derived character in scorpaeniform fish according to Washington et al. (1984b). By contrast, the presence of both a reduced fifth hypural element (HY_5) and a parhypural element represents a plesiomorphic condition, which in turn suggests that this monospecific genus still retains characters that correspond to a more generalized type of scorpaenid. More information is needed, however, on related genera of the Scorpaenidae to provide a more detailed comparison of these characters in larval *G. marmoratus* and to suggest relationships within the suborder Scorpaenoidei.

Distinguishing Larval Characters

Larval *G. marmoratus* can be distinguished from other scorpaenid larvae that occur within its geographical range by the possession of 29 myomeres, the dorsal fin count of XIII, 9, and their large and distinctively pigmented fan-shaped pectoral fins which form early in development. Larvae of *Scorpaena* are distinguished

from *G. marmoratus* by a lower number of myomeres, whereas *Maxillicosta* and *Neosebastes* possess a higher number of pectoral fin rays (18–21) (Scott et al. 1980; Leis and Rennis 1983). Larvae of *Centropogon* and *Glyptauchen* are distinguished from *G. marmoratus* by their possession of a higher number of spines (15–18) in the dorsal fin (Washington et al. 1984b). Juvenile *G. marmoratus* can also be distinguished from other known scorpaenids in the area by their distinctive head spination and scaleless skin (Hutchins and Thompson 1983).

Larvae of *G. marmoratus* can be confused with some platycephalids and triglids, which also have pigmented pectoral fins and well-developed head spination. However, platycephalid larvae have numerous small melanophores scattered over the body surface, depressed heads with flattened snouts, and smaller parietal spines (Leis and Rennis 1983). Triglid larvae can be distinguished from *G. marmoratus* by the depressed profile of their heads and by large pectoral fins in which the lowest three rays become detached during transformation (Washington et al. 1984a).

Occurrence of Larvae in the Swan Estuary

Gymnapistes marmoratus larvae were found in surface waters of the Swan Estuary between July and September 1986, and peak numbers were obtained in July (Neira, unpubl. data). Larvae were collected in the area of the lower Swan Estuary located between 3.0 and 9.0 km upstream from the estuary mouth. The transforming larva and juveniles from the Peel-Harvey Estuary were collected by beach seines in October and August 1985 respectively. The occurrence of larvae and juveniles from both estuaries indicates that a population of *G. marmoratus* from southwestern Australia spawns in late winter and early spring. This spawning period is coincident with that reported in other regions of southern Australia such as Tasmania (Grant 1972), Port Phillip Bay (Jenkins 1986), and the Gippsland Lakes (Ramm 1986).

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I would like to thank B. B. Washington, J. M. Leis, and I. C. Potter for their helpful comments on the manuscript. Thanks are also due to D. Gaughan, L. E. Beckley, and M. Cliff for their help in the collection of the larvae. This research was carried out during the term of a Murdoch University Research Studentship given to the author.

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New Squat Lobsters (Galatheidae) from the Pacific Ocean: Mariana Back Arc Basin, East Pacific Rise, and Cascadia Basin

Austin B. Williams and Keiji Baba

ABSTRACT: Three species of squat lobsters new to science are described and illustrated. *Munidopsis marianica*, collected with the aid of DSRV *Alvin* from a hydrothermal vent area in the Mariana Back Arc Basin in the western Pacific, is distinguished from a northeastern Pacific species, *M. tuftsi* Ambler, by the erectness of its eye spines and ornamentation of the body, form of telson plates, and spination of dactyls on walking legs. *Munidopsis lignaria*, collected in association with submerged wood with the aid of RV *Yaquina* in trawl samples from the eastern Pacific Cascadia Basin off Oregon and DSRV *Alvin* from the East Pacific Rise off south central Mexico, is distinguished from its nearest congener, *M. ciliata* Wood-Mason, by blunter ornamentation and smaller body size. *Munidopsis granosicorium* from Cascadia Basin is represented by a unique specimen, the carapace of which has a distinctive unspined ornamentation but a much more broadly triangular rostrum and more pronounced anterior elevation than that of its apparent closest relative, *M. follirostris* Khodkina.

On a recent *Alvin/Atlantis II* expedition to the Mariana Back Arc Basin in the western Pacific, 28 dives were made, 6 of them entirely devoted to biology. Those dives focused on 3 active low temperature (10°–25°C) vent sites at which anemones, mollusks, shrimps, squat lobsters, crabs, and other invertebrates were observed or collected (R. Hessler[1]; Hessler et al. 1988). We here describe a new species of *Munidopsis* collected during 3 of the dives.

A subsequent *Alvin/Atlantis II* expedition (Cruise 118, Leg 32) focused on geological exploration of the East Pacific Rise between lat. 10°55′N and 11°55′N. Small fields of past and present hydrothermal activity were found along the axis of this region, and among samples of biological specimens collected from both vent and nonvent environments was a piece of wood colonized by a variety of invertebrates, including a species of *Munidopsis* (see Van Dover 1988). These specimens are identical to specimens taken during extensive collections of benthic megafauna made at stations of the RV *Yaquina* on the Oregon continental margin and nearby abyssal plains from 1962 to 1983 (Ambler 1980; Carney and Carey 1982; Carey[2]). A pattern of stations was sampled to determine the distribution and abundance of mega-epifauna and to study the ecological influence at sea of radionuclides originating from the Hanford (WA) Nuclear Reservation. Collections at these and other study areas in the region were made with a 7.1 m semiballoon otter trawl (1.3 cm mesh) and with a 3 m beam trawl (1.3 cm mesh) equipped with paired odometer wheels (Carey and Heyamoto 1972). We reviewed all of this material and here describe the species as new. Finally, a unique but fragmentary specimen of *Munidopsis* from Professor Carey's sampling program is described.

Specimens studied, except where otherwise indicated, were from the Oregon State University Benthic Invertebrate Museum (OSUBI), Corvallis, OR; the Museum of Comparative Zoology, Harvard University (MCZ), Cambridge, MA; and the Division of Crustacea of the United States National Museum of Natural History, Smithsonian Institution (USNM), Washington, DC. Types of new species are deposited in crustacean collections of the USNM and OSUBI.

Munidopsis marianica New Species

Figures 1, 2*a*, 3*a*, *b*

Material studied.—Western Pacific Ocean,

[1]Robert Hessler, Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun. September 1987.

[2]A. G. Carey, Jr., College of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. September 1988.

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Keiji Baba, Kumamoto University, Faculty of Education, Kurokami 2-chome, Kumamoto, 860 Japan.

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Fishery Bulletin, U.S. 87: 899–910.

Mariana Back Arc Basin. USNM 240198. Holotype ♀ (ovig.). Burke Field, 18°11′N, 144°43′E, 3,680 m, *Alvin* Dive 1837, 28 April 1987, Pilot Salzig, Observers Hessler, France.—USNM 240199. Paratypes, 2 ♀ (ovig.), 1 ♂, same.—USNM 240200. Paratype ♀. Illium, 18°15′N, 144°42′E, 3,620 m, *Alvin* Dive 1829, 14 April 1987, Pilot Tibbets, Observers Craig, Farley.—USNM 240201. Paratype ♀. 18°11′N, 144°43′E, 3,727 m, *Alvin* Dive 1847, 8 May 1987, Pilot Salzig, Observers J. and D. Hawkins; transferred to collection of the Zoological Laboratory, Kyushu University (ZLKU). The material was graciously donated to us by R. Hessler, Scripps Institution of Oceanography, La Jolla, CA.

Measurements in mm.—Holotype ♀ (ovig.), carapace length including rostrum 52.1, margin of orbit to posterior edge of carapace 38.0, maximum carapace width 30.8; same (respectively). Paratypes USNM 240199, ♀ (ovig.) 33.9, 25.6, 21.8, ♀ (ovig.) 36.0, 25.8, 21.1, ♂ 26.2, 19.0, 15.3; USNM 240200, ♀ 40.7, 30.2, 26.0; USNM 240201, ♀ 38.0, 28.1, 23.7.

Description.—Carapace (Fig. 1*a–c*) exclusive of rostrum distinctly longer than broad, moderately arched transversely; anterior and posterior cervical grooves apparent, transverse depression in anterior part of cardiac region. Rostrum almost horizontal, narrow to moderately broad triangular, lateral margin with denticles on distal third, tip exceeding eyestalks by more than their length, variably obscure to distinct dorsal carina bearing obsolescent tiny tubercles that merge into median tubercles on gastric region. Slightly raised concave frontal margin sweeping to antennal spine followed by irregularly oblique margin leading to acutely spined anterolateral angle. Gastric region somewhat inflated but slight posterolateral concavity at either side defining meso-metagastric area; anterior gastric region bearing moderate spine on either side of midline, and lateral to each another variably developed spine in moderately arched transverse row; remainder of gastric region lightly rugose. Anterior branchial region bearing strong anterolateral spine followed by 5 or 6 successively diminishing lateral spines, and scattered moderate tubercles dorsally. Short rugae and obscure tubercles clustered behind juncture of anterior and posterior cervical grooves. Posterior branchial region bearing strong anterolateral angle, sometimes spiniform, and distinct oblique and transverse rugae laterally; rugae with tendency to being transversely continuous across central part of cardiac region. Posterior margin concave, preceded by narrow raised rim with slightly cupped crown. Lateral plate obliquely rugose, projecting anteriorly below antennal peduncle; rugosities on anterodorsal margin minutely serrated, and angular anterior tip bearing minute spine.

Abdomen (Fig. 1*a*) unarmed; transverse ridge of segments 2 and 3 smooth, divided into narrow anterior and broader posterior parts by concave trough, that of segment 4 obsolescent; segments 5 and 6 smooth, 6 slightly raised posteriorly in middle, posteromedian margin strongly produced, overreaching lateral lobe on each side. Telson divided into 8 plates (Fig. 2*a*), length-width ratio 0.79 ± SD 0.052, $n = 6$, midlateral plate markedly convex on distolateral margin.

Eyes (Figs. 1*b, c*, 3*a*) moderate in size; well exposed, smoothly ovate cornea cupped within movable broad-based ocular peduncle; peduncle extended into strong mesiodorsal spine directed horizontally or obliquely upward at very low angle and ornamented with tiny, irregular, obsolescent spinules; a much shorter lateral spine near base of cornea; behind that an alate basal process, either acutely spined or multispinose at tip, posterolaterally paralleling concave frontal margin.

Basal article of antennular peduncle with distal margin irregularly crenulate; slender dorsolateral carina continued into anterior spine, below it a broader anterior spine directed obliquely laterad, flanked by inflated surface bearing cluster of irregular small spines or spinules; mesiodorsal spine much smaller. Antennal peduncle with fixed basal article extended into stout, flat ventral spine with subdivided mesial margin and shorter, sometimes crenulate, lateral spine; succeeding articles short, second bearing appressed lateral angle, third with serrate distal margin, fourth with scalloped distal margin.

Third maxilliped (Fig. 1*d*) with ischium shorter than merus; bearing mesial crest armed with finely uniform, evenly spaced corneous tipped spines and a distodorsal spine. Basis with 3 or 4 corneous spines similar to and in line with crest on ischium. Merus with 6 irregular acute spines on flexor margin and strong spine at distodorsal corner. Carpus, propodus, and dactyl folded on merus-ischium and about as long as those 2 articles together, flexor surface of each bearing dense setation mesially, and distally on propodus

and dactyl. Sternite at base of third maxilliped (Fig. 1*e*) forming apposed lobe at either side of midline, outline of each irregularly polygonal but with anteromesial process irregularly serrate on margin and divergent.

Epipod on coxa of first pereopod (cheliped), but rudimentary on left side and absent on right side of paratype USNM 240201.

Chelipeds (Fig. 1*f*) subequal, with many spines and fewer rugosities tending to arrangement in longitudinal tracts; ischium with mesial row of 8 acute spines, irregular smaller spines on distoventral margin, and smaller spines and rugosities ventrally; merus reaching end of rostrum, bearing row of 7 mesial spines, terminal one strongest, about 10 spines along

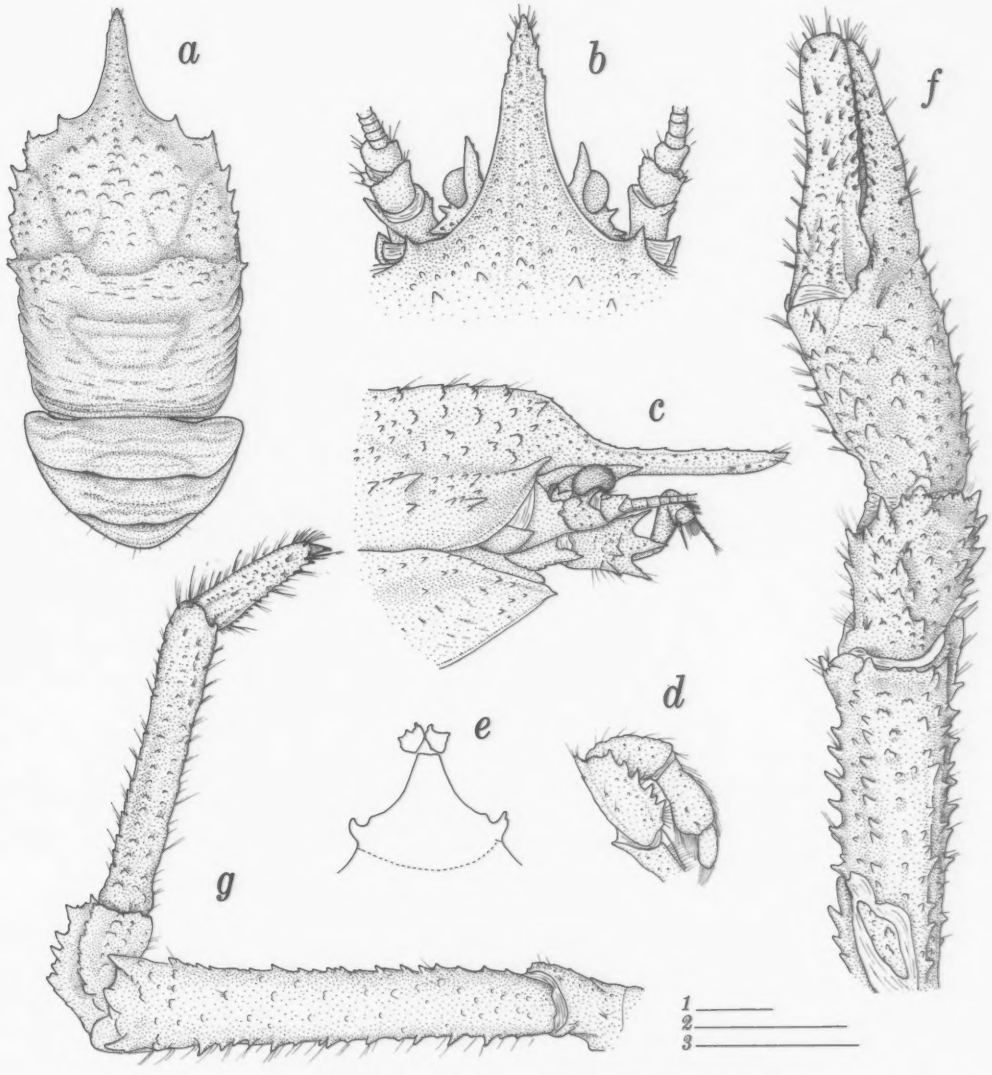

FIGURE 1.—*Munidopsis marianica*, holotype ♀: *a*, carapace, abdominal segments 2–4 in folded position, dorsal; *b*, parts of anterior carapace and associated appendages, dorsal; *c*, parts of anterior cephalothorax and associated appendages, lateral; *d*, merus of right third maxilliped with parts of adjacent articles; *e*, sternites at base of third maxillipeds and chelipeds; *f*, right cheliped; *g*, left first walking leg. Scales: 1(*a*), 2 (*b*, *c*, *f*), 3 (*d*, *e*, *g*) = 10 mm.

lateral margin; carpus spiny except on ventral surface; palm strongly spiny on mesial and lateral surfaces, less so dorsally but with scattered rugosities there as well; fingers about as long as palm, spooned, especially at tips, prehensile edges almost entire but imperceptibly crenulate, tips close fitting.

Walking legs rather long, first walking leg (Fig. 1*g*) reaching almost to tip of chela, second and third walking legs reaching almost to base of dactyl on preceding leg (right second walking leg missing from holotype); corresponding articles of respective legs approximately equal in length except for meri which decrease posteriorly; each merus with spiny dorsal crest ending in strong distal spine; prehensile surface with 2 rows of rugae, spines, and tubercles; carpi each with longitudinal dorsal and lateral rib, each ending in

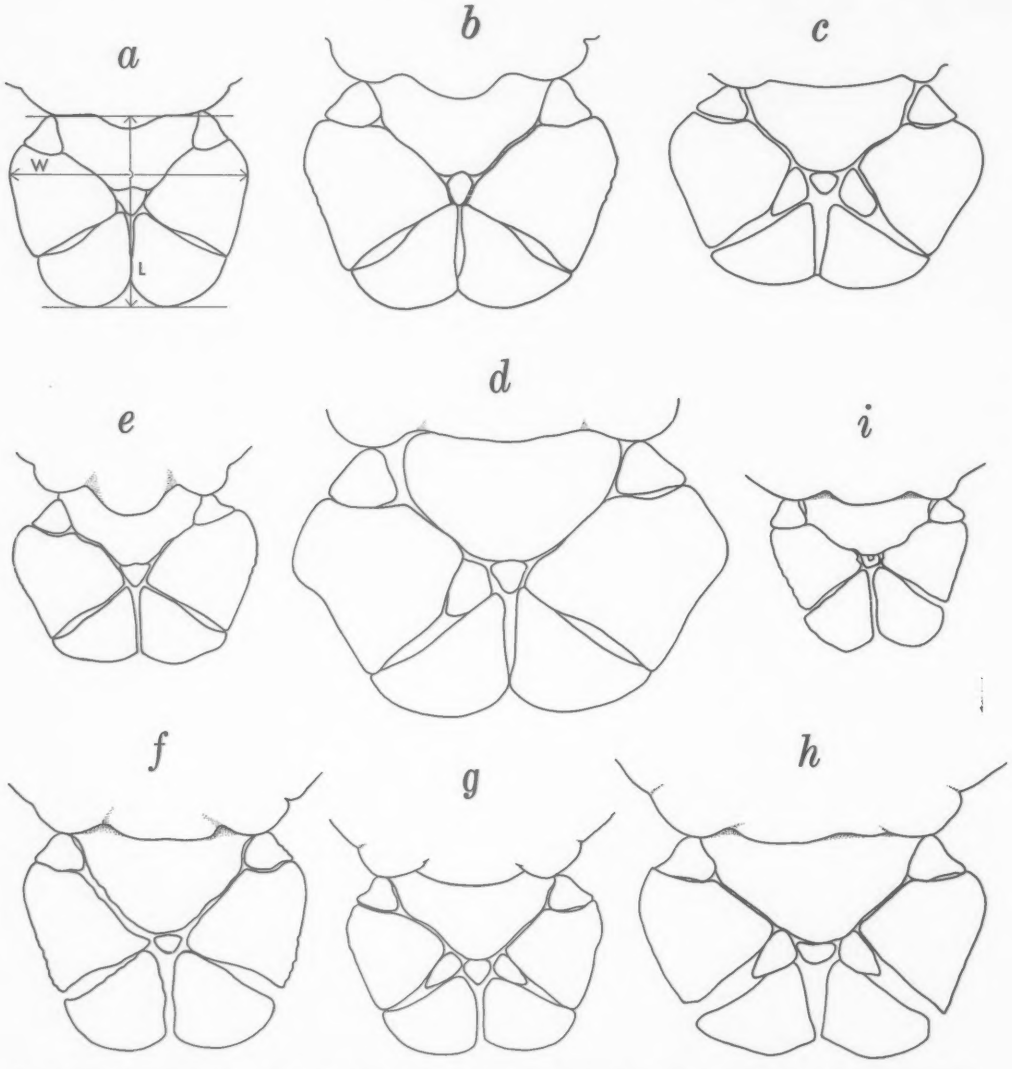

FIGURE 2.—Outlines of telson plates and distal margin of abdominal segment 6, lines on *a* indicate pattern for length (L) and width (W) measurements: *a*, *Munidopsis marianica*, paratype + USNM 240201; *b*, *M. tuftsi*, holotype ♂, USNM 171336; *c*, *M. subsquamosa*, syntype BM 88:33; *d*, *M. subsquamosa aculeata*, holotype ♂, BM 88:33; *e*, *M. crassa* holotype ♀, USNM 8536; *f*, *M. lignaria*, holotype ♂, USNM 240202; *g*, *M. ciliata*, ♀, USNM 151856, Celebes, Indonesia; *h*, *M. nitida*, ♂, USNM 150580, St. Croix Basin, Caribbean Sea, note atypically sinuous terminal margin on median lobe of segment 6; *i*, *M. granosicorium*, holotype ♀, USNM 240205.

well-developed terminal spine, and with secondary spine on distal margin between them, dorsal rib spiny, lateral rib less so; each propodus slender, with dorsal, dorsolateral, and lateral ridges spiny in proximal half but less so distally, dorsal spines pronounced; each dactyl slender, acute corneous tip preceded by row of 14 or more movable spines on prehensile edge. Chela on slender fifth leg with well-developed cleaning brush (chelae missing on holotype).

Eggs on holotype ♀ few, large, principal axes measuring 1.3 × 1.6 mm.

Remarks.—Observations televised during *Alvin* Dive 1845, 18°13′N, 144°42′E, 3,716 m, 6 May 1987, Pilot Hollis, Observers Ohta, Kono, included views of *Munidopsis* that may be this species.

Munidopsis marianica resembles a number of species in the genus that normally have epipods restricted to the first pereopods, eyespines extending beyond the cornea, and chelipeds lacking a denticulate carina on the distolateral margin of the chela, including *M. crassa* Smith, 1885; *M. similis* Smith, 1885; *M. subsquamosa* Henderson, 1885; *M. barnardi* Kensley, 1968; *M. tuftsi* Ambler, 1980; and *M. geyeri* Pequegnat and Pequegnat, 1970. *Munidopsis similis*, originally considered to be a variety (subspecies) of *M. crassa* (see Smith 1885:496), is different from this group in lacking epipods on all pereopods (Pequegnat and Pequegnat 1970:139). *Munidopsis geyeri* was synonymized with *M. subsquamosa* (see Ambler 1980:26), and *M. barnardi* from South Africa (Kensley 1968:290) will in all probability be merged with *M. subsquamosa* (unpubl. data). Therefore, the remaining three species are compared with the present new species.

The closest relative to this new species seems to be *M. tuftsi*, known from off Oregon (Ambler 1980:24). The shared characters are relatively long chelipeds, particularly meri that extend nearly to the rostral tip, the anterior half of the carapace that bears tubercles or spines rather than rugae, and the strongly convex posteromedian margin of the sixth abdominal segment that distinctly overreaches the lateral lobe on each side. However, *M. tuftsi* differs from *M. marianica*—the walking legs are more strongly spinose but the chelipeds are less spiny; the anterior half of the carapace, especially the anterior branchial region, bears distinct dorsal spines; the telson is relatively wide (length-width ratio, 0.71 in the holotype of *M. tuftsi*, 0.79 [$\bar{x}$] in *M. marianica*), the midlateral plate is more markedly convex on the distolateral margin; and the rostrum is distinctly carinate dorsally, relatively high and strongly upcurved. Most clearly different in the 2 species are dactyli of the walking legs (Fig. 3*b*, *c*); they terminate in a short corneous, curved spine. In *M. tuftsi*, the ultimate ventral tooth is distinctly closer to the tip of the terminal spine than to the penultimate

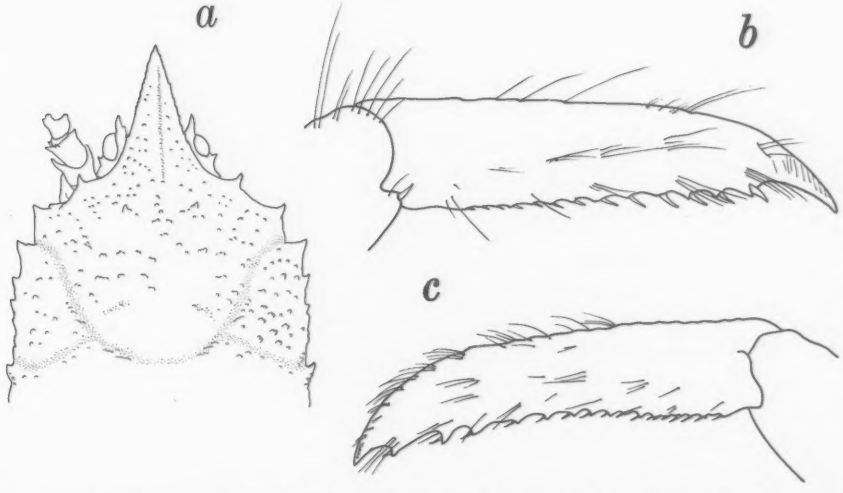

FIGURE 3.—*Munidopsis marianica*, paratype ♀, USNM 240201: *a*, anterior carapace with parts of appendages, dorsal; *b*, dactyl of first walking leg; *c*, *M. tuftsi*, holotype ♂, USNM 171336, dactyl of first walking leg.

ventral tooth, while in *M. marianica* the terminal spine is elongate and the ultimate ventral tooth is nearer to the penultimate one. The above listed differences were confirmed by examination of the holotype of *M. tuftsi* (USNM 171336) as well as an additional male specimen of *M. tuftsi* taken at *Galathea* station 450 in the Celebes Sea (unpubl. data).

Munidopsis subsquamosa and *M. crassa* are also similar to *M. marianica*. General characteristics of *M. subsquamosa* were examined on 2 snytypes (♂, and softened remains, BM 88:33; and the holotype ♂ of *M. subsquamosa aculeata*, BM 88:33), both described by Henderson (1885, 1888) now deposited in the British Museum (Natural History), and on 2 examples of *M. subsquamosa* taken rather near its type locality by the *Soyo Maru*, reported earlier by Baba (1982:114). Examined also were the abdominal fragment of the holotype of *M. crassa* (USNM 8536) in which both the telson and the sixth abdominal segment are intact, and 2 specimens (1 ♂, 1 ♀) referable to *M. crassa* (USNM 231328) that taken by the RV *Alvin* from the North Atlantic Ocean southeast of Massachusetts (lat. 38°18′24″N, long. 69°35′30″W, 3,506 m) very near the type locality. The anterior branchial region of the carapace usually bears elevated, scalelike striae in *M. subsquamosa* instead of tubercles or spinules as in *M. crassa* and *M. marianica*. The posteromedian margin of the sixth abdominal segment is feebly convex and never exceeds the end of the lateral lobes in *M. subsquamosa*, but it is markedly produced, overreaching the lateral lobes in *M. crassa* and *M. marianica*. The telson (Fig. 2*a–e*) is relatively narrower in *M. marianica* (length-width ratios: 0.61–0.65 in *M. subsquamosa*; 0.68–0.70 in *M. crassa*; 0.79 [$\bar{x}$] in *M. marianica*). The fingers of the cheliped are distally narrowed in *M. subsquamosa* and *M. crassa*, but uniformly wide throughtout the length so as to form a sharply defined ventral spoon in *M. marianica*. The merus of the cheliped in *M. subsquamosa* and *M. crassa* is middorsally ridged, more sharply so toward the proximal end, instead of being bluntly ridged as in *M. marianica*. The mesial eyespine is directed anterolaterad in *M. subsquamosa* and *M. crassa*, while in *M. marianica* it is directed nearly straight forward. The rostrum is straight and horizontal in *M. marianica*, but usually curving dorsad in *M. subsquamosa* and *M. crassa*. Finally, the merus of the third maxilliped is more spinose on the flexor margin in *M. marianica* (bearing about 6 spines) than in *M. crassa* and *M. subsquamosa* (3 or 4 spines).

Etymology.—Named for the type locality.

Munidopsis lignaria New Species

Figures 2*f*, 4

Munidopsis ciliata, Ambler, 1980:19, fig. 4.—not *M. ciliata* Wood-Mason *in* Wood-Mason and Alcock, 1891:200.

Munidopsis sp. Van Dover, 1988:6, unnumbered fig.

Material studied.—Eastern Pacific Ocean, Cascadia Basin off Oregon: USNM 240202. Holotype ♂. 44°39.8′N, 125°36.4′W, 2,875 m, RV *Yaquina* cruise Y 7001 B, stn CP-1-E, BMT 184, 16 March 1970, transferred from OSUBI 00188.—USNM 240203. Allotype ♀. 45°18.6′N, 126°31.5′W, 2,750 m, RV *Yaquina* cruise Y 7001 B, stn CP-2-C, BMT 265, 18 February 1971, transferred from OSUBI 01578.—OSUBI 00189. Paratypes, 19 ♂, 13 ♀. 44°53.7′N, 126°33.4′W, 2,774 m, RV *Yaquina*, cruise Y 7001 B, stn CP-2-D, from log collected in beam trawl 162, 19 January 1970.—USNM 171342. Paratype ♀. 45°55.3′N, 125°36.1′W, 2,030 m, RV *Yaquina* cruise Y 7003B, stn CP-1-A, BMT 194, 20 March 1970.—USNM 171343. 6 ♂, 7 ♀. 45°52.5′N, 126°40.8′W, RV *Yaquina* cruise Y 7001 B, stn CP-2-A, BMT 154, 16 January 1970.

East Pacific Rise off south central Mexico: USNM 240204. Paratypes, 8 ♂, 12 ♀. Western limb of overlapping spreading center near 11°52′N, 103°51′W, 2,750 m, *Alvin* Dive 2000, 22 March 1988, from a piece of wood measuring about 15 × 30 cm, Pilot Ralph Hollis, Observers W. Bryan and R. Hekinian (IFREMER). This material was donated to us by Cindy Van Dover, Woods Hole Oceanographic Institution, Woods Hole, MA.

Measurements in mm.—Holotype ♂, carapace length including rostrum 15.0, margin of orbit to posterior edge of carapace 10.2, maximum carapace width 9.0; Allotype ♀, same (respectively), 16.5, 11.6, 10.2; smallest Paratype ♂, USNM 240204, same 9.0, 6.7, 6.3; smallest Paratype ♀, USNM 240204, same, 9.2, 6.5, 5.5.

Description.—Carapace (Fig. 4*a–b*), exclusive of rostrum, longer than broad, moderately arched transversely; anterior and posterior

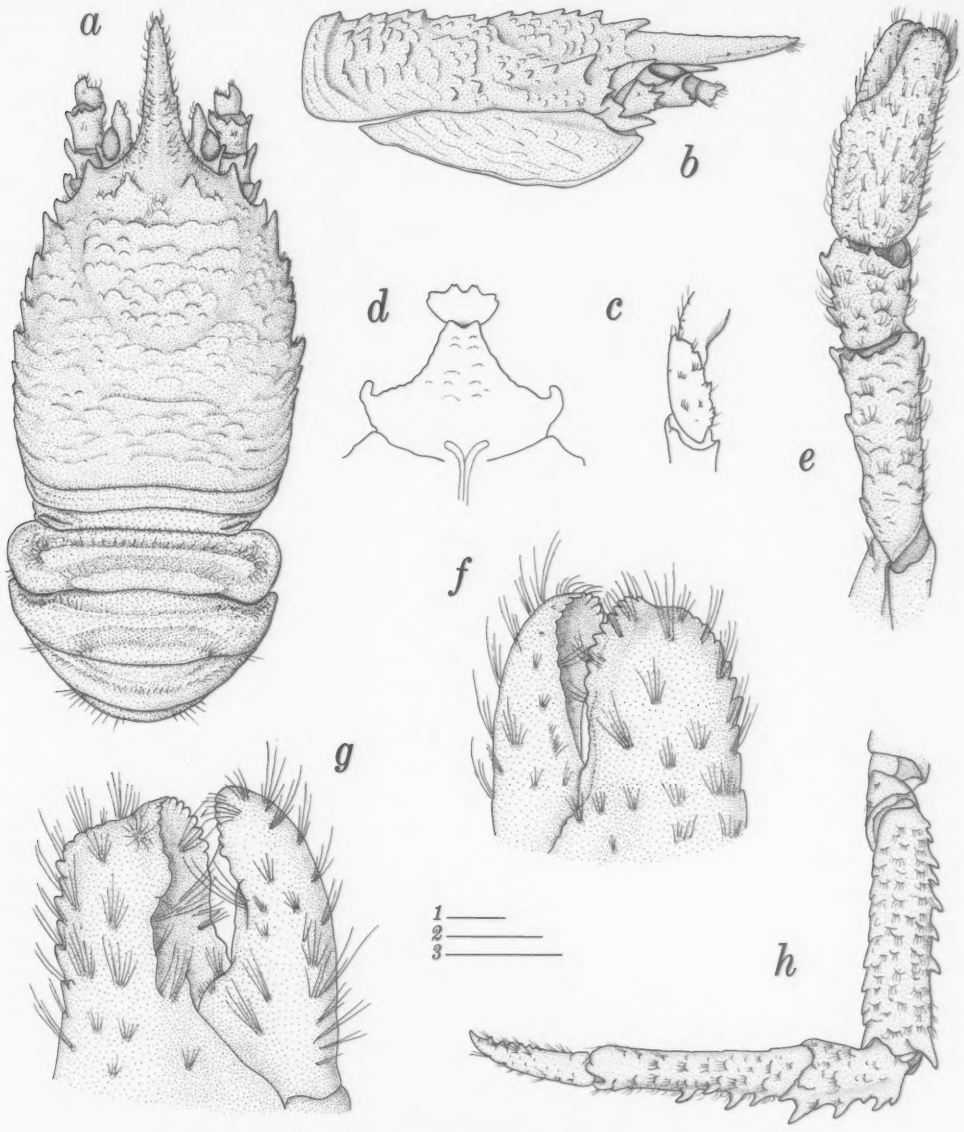

FIGURE 4.—*Munidopsis lignaria*, holotype ♂, USNM 240202: *a*, carapace and parts of anterior appendages, abdominal segments 2–4 in folded position, dorsal; *b*, cephalothorax and parts of anterior appendages, lateral; *c*, merus of right third maxilliped and parts of adjacent articles; *d*, sternites at base of maxillipeds and chelipeds; *e*, right cheliped, and views of fingers; *f*, dorsal; *g*, ventral. Scales: 1(*c*, *d*), 3(*f*, *g*) = 1 mm, 2(*a*, *b*, *e*, *h*) = 3 mm.

cervical grooves apparent, transverse depression in anterior part of cardiac region. Rostrum narrowly triangular, tip exceeding eyestalks by their own or slightly greater length; horizontal dorsal surface nearly smooth, with low but distinct carina becoming obsolescent between prominent gastric spines. Frontal margin with acuminate, slightly hooked antennal spine lateral to eyestalk followed by concavity ending in small, acute anterolateral angle. Gastric region bearing short setose rugosities arranged in more or less concentric arcs behind strong gastric spine at either side of midline (reduced secondary gastric spine lateral to each in large indi-

viduals). Anterior branchial region bearing less prominent ciliated rugosities, its lateral margin with strong anterior spine followed by 4 spines successively smaller in size. Posterior branchial region with moderately developed spine at anterolateral corner and more distinct and transversely developed setose rugae, with tendency in larger adults for these to be most elongate across anterior and central part of cardiac region. Shallowly concave posterior margin preceded by prominent raised, ciliated submarginal rim of nearly uniform width. Lateral plate obliquely rugose, projecting anteriorly below antennal peduncle, its rather rounded tip bearing minute spine.

Abdomen (Fig. 4*a*) unspined, but segments 2 and 3 boldly ridged transversely; ridging of segment 4 transitional; segments 5 and 6 smooth, latter with posterior margin trilobate, distal margin of lateral lobes convex, that of broader median lobe very shallowly concave. Telson (Fig. 2*f*) composed of 8 plates, length-width ratio in holotype 0.85, in smaller ♀ paratype 0.83, midlateral plate convex on distolateral margin.

Eyes (Figs. 4*a–b*) moderate in size; well exposed, smoothly ovate cornea cupped within broad-based slightly movable ocular peduncle extended into elongate mesiodorsal spine; spine horizontal or directed obliquely upward at low angle; peduncle ornamented with few setae and tiny irregular obsolescent spinules, much shorter mesioventral spine, and intermediate length lateral spine.

Basal article of antennular peduncle with crested dorsal margin minutely and irregularly serrate, extended into slender dorsolateral spine, broader lateral spine below, base of each flanked laterally by cluster of irregular, small, obsolescent spinules on inflated lateral side of article; mesial edge with crenulate scalloped margin. Antennal peduncle with fixed basal article extended into stout, flat, ventral spine and shorter lateral spine with crenulate margin; succeeding articles short, second bearing slender lateral angle, third with scalloped and crenulate distal margin, fourth with scalloped distal margin, its dorsolateral projection stoutly spinelike.

Third maxilliped with ischium shorter than merus; bearing mesial crest armed with finely uniform, evenly spaced corneous-tipped spines; anteroventral angle acute. Basis with 2 low spines in line with crest on ischium. Merus (Fig. 4*c*) with few obsolescent spines preceding 3 principal spines on flexor margin, proximal and middle spines incompletely doubled; extensor margin broadly arched, strong, acute spine at anterodistal corner. Carpus, propodus, and dactyl folded on merus-ischium and about as long as those 2 articles together, dense setation on dorsal surface of each, and distally on flexor surface of propodus and dactyl. Sternite at base of third maxilliped (Fig. 4*d*) with crenulate anterior margin on angular mesial and lateral lobes.

Epipod present on first pereopods (chelipeds).

Chelipeds (Fig. 4*e–g*) stout, subequal, ornamented with moderately developed, variably setose rugosities tending to arrangement in longitudinal tracts; ischium with short lateral spine and mesial ridge bearing obsolescent subterminal spines; merus bearing 3 principal mesial spines, 1 distodorsal spine, and distoventral spine on mesial and lateral margins; carpus with dorsolateral row of tubercles and mesiodorsal row of 3 spines; palm nearly smooth, few obsolescent tubercles on dorsomesial surface; stout fingers shorter than palm, spooned at tips, prehensile edges close fitting, crenulate; crest of small spines at distolateral angle of fixed finger.

Walking legs rather long, first walking leg (Fig. 4*h*) exceeding tip of chela, second and third reaching to near base of dactyl on preceding leg; corresponding articles of respective legs approximately equal in length except for meri which successively decrease posteriorly; each merus with crest on dorsal margin ending in distal spine, and corresponding crest on ventrolateral margin; carpi with longitudinal spiny dorsal and tuberculate dorsolateral crest, each ending in more or less well-developed spine; each propodus slender, bearing crests in line with those of carpus, dorsal crest bearing 2 remote spines in proximal half, each with small movable spine distolaterally at base of dactyl, another sometimes preceding it in distal ⅓ of length, and smaller movable spine at distomesial corner; each dactyl slender, acute corneous tip preceded by row of 10–12 movable spines on flexor margin. Slender, chelate fifth leg with well-developed cleaning brush on palm and somewhat pointed but flattened dactyl opposed by similar setae on distal end of propodus.

Variation.—There is minor variation in ornamentation of the specimens available for study, large adults being relatively more coarsely ornamented than smaller individuals.

Remarks.—*Munidopsis lignaria* is allied to *M. ciliata* Wood-Mason of the western Indo-Pacific,

M. nitida (A. Milne-Edwards, 1880) of the western Atlantic, and more distantly, *M. verrilli* Benedict, 1902 of the eastern Pacific. Ambler (1980:19) correctly differentiated, from *M. ciliata*, the new species with "shorter, stouter spines on the carapace and legs; shorter setae covering the carapace and legs; rostrum with a narrower base; and no extra spine between the anterolateral and antennal spines, as sometimes occurs in the *Albatross* specimens." However, she regarded the differences between these 2 forms as racial or varietal rather than specific, a view paralleling that of Faxon (1895:84), who identified eastern Pacific specimens collected by the *Albatross* as *M. ciliata*, and stated that differences between *M. nitida* and *M. ciliata* "appear to be of racial or varietal, rather than specific, value." However, he reserved judgment until the distribution of each might become better known. It does appear that the specimens seen by Faxon closely resemble *M. ciliata*, although only those from *Albatross* stations 3392 and 3393 are now present in the MCZ crustacean collection, and there is no record of specimens from stations 3353 and 3363 in the MCZ crustacean catalog[3]. There are minor differences in spination of the walking legs of *M. ciliata* and those of the available specimens seen by Faxon, but before deciding the status of this eastern Pacific material a search for the missing material should be made.

Munidopsis ciliata reaches noticeably larger size as an adult than does *M. lignaria*. *Munidopsis ciliata* is characterized by much longer and more slender spination, and much longer and more prominent setae springing from rugosities of the carapace and legs than on *M. lignaria*.

Munidopsis nitida has well-developed acute spines on legs and cephalothorax, but rugae are far less prominent than in either *M. ciliata* or *M. lignaria*, and unlike either of these has the rostrum upturned distally at a low angle.

Munidopsis ciliata, *M. lignaria*, and *M. nitida* have a distally trilobate margin on the sixth abdominal segment (Fig. 2*f–h*), each with a convex lobe to either side and a broader median lobe; the middle portion of the median lobe of *M. lignaria* usually has a very shallowly concave distal margin, that of *M. ciliata* is slightly convex and slightly arched dorsally, and that of *M. nitida* is almost transversely straight except for a slight concavity at either side where it joins the respective lateral lobes. *Munidopsis lignaria* has 8 plates in the telson (Fig. 2*f*) whereas the other species have 10. The telson of *M. lignaria* has a length-width ratio of 0.85 in the holotype, and 0.83 in a much smaller paratype; that ratio in *M. ciliata* is 0.70, and in *M. nitida* it is 0.72.

The chelae of these 3 species are similar, having close fitting, crenulate distal edges on the tips of the spooned fingers, and a serrate distolateral angle on the fixed finger. Width-length ratios of the chelae are 0.50 in *M. lignaria* and *M. ciliata*, and 0.41 in *M. nitida*. Both *M. lignaria* and *M. nitida* have been collected in association with wood (see material studied; Williams and Turner 1986), and Van Dover (1988) found numerous wood fragments in the stomachs of *M. lignaria* collected off Mexico. The chelae of the latter 2 species look as if they could be used for boring, tunneling in, or shredding wood. There are no published habitat data for *M. ciliata*. However, Wolff (1979) recorded the association of *M. vicina* Faxon, 1895, *M. hendersoniana* Faxon, 1895, and *Munidopsis* sp. with wood. The first two of these species, having chelae similar to those discussed here (see Faxon 1895: pl. XVIII, fig. 2*a* and pl. XXIV, figs. 2, 2*c*) were listed as utilizing wood for food, and the third sheltering in it.

Munidopsis verrilli, with which Ambler (1980) also compared the new species, is much more distant, being a larger species with conspicuously setose legs, relatively longer and stronger chelipeds lacking epipods, more coarsely ornamented cephalothorax with rugosities in a different pattern on both carapace and side plates, a relatively shorter rostrum, and more globose eyes from the margin of which the 3 spines project prominently at divergent angles, to mention the most obvious differences.

Etymology.—From the Latin "lignarius", of or belonging to wood, for the association of the species with pieces of wood.

Munidopsus granosicorium New Species

Figures 2*i*, 5

Material studied.—USNM 240205. Holotype ♀ (ovig.), eastern Pacific Ocean off Strait of Juan de Fuca, 48°38.7′N, 126°57.6′W, 2,020 m, RV *Destiger*, DWD-BMT 10, 11 September 1971.

Measurements in mm.—Carapace length including rostrum 9.7, margin of orbit to posterior

[3]Ardis B. Johnston, Harvard University Museum of Comparative Zoology, Cambridge, MA 02138, pers. commun. October 1988.

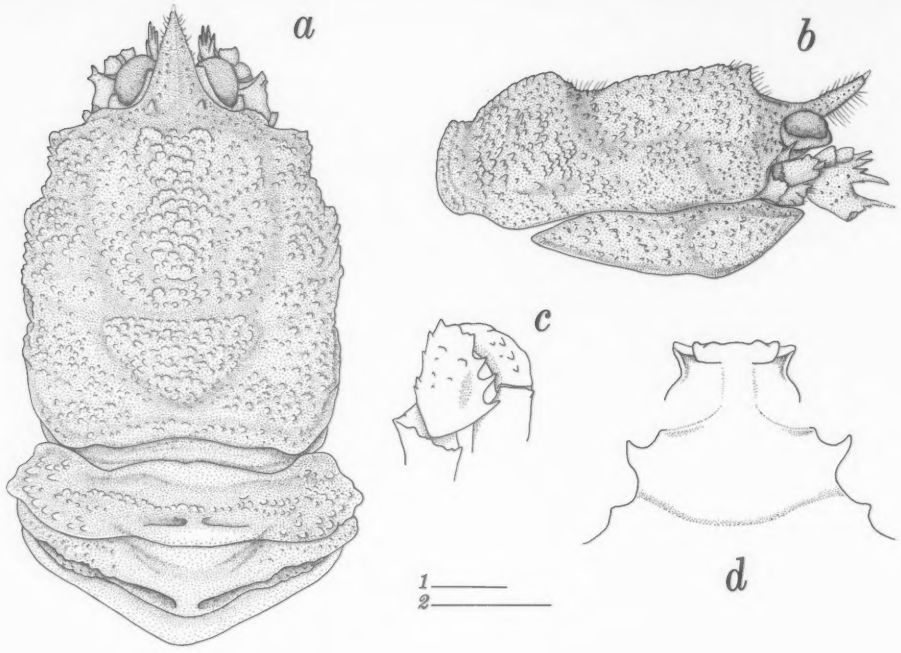

FIGURE 5.—*Munidopsis granosicorium*, holotype ♀, USNM 240205: *a*, carapace and parts of anterior appendages, abdominal segments 2–4 in folded position, dorsal; *b*, cephalothorax and parts of anterior appendages, lateral; *c*, merus of right third maxilliped and parts of adjacent articles; *d*, sternites at base of maxillipeds and chelipeds. Scales: 1(*c*, *d*) = 1 mm, 2(*a*, *b*) = 3 mm.

edge of carapace 7.4, maximum carapace width 7.7

Description.—Integument iridescent. Carapace (Fig. 5*a*, *b*), exclusive of rostrum approximately as long in midline as broad, sculptured, variably ridged longitudinally; anterior and posterior cervical grooves apparent but obscure, prominent transverse ridge across anterior part of raised cardiac region; crowded rugae on dorsal surface moderately elevated, most closely clustered and transversely elongated on median prominences, especially on cardiac region, giving an overall uneven, variably pebbled appearance; a nearly smooth and slightly concave spot to either side of midline at anterolateral corner of cardiac region. Rostrum broadly subtriangular, transversely arched, base broader than midsagittal length; dorsal surface in lateral view with concave base smoothly curving into upwardly inclined distal part having almost straight dorsal margin, apparently acute tip slightly blunted by damage; lateral margins anterior to eyes serrate, but concave posterior margins adjacent to eyes nearly smooth; scattered tubercles on anterior ⅝ of length much smaller and more numerous than larger, symmetrically arranged rugae on posterior ⅜; anterior part with noticeable brush of plumose setae, densest ventrally. Sinuous frontal margin with broad angle lateral to eyestalk continued laterad as thin raised edge curving into a small serrate lobe proximolateral to basal article of antenna; anterolateral angle densely and sharply rugose, followed by similar but somewhat more broadly projecting lateral margin of anterior branchial region, margin thinner on posterior branchial region. Posterior margin broadly and shallowly concave, slightly sinuous; preceded in turn by submarginal narrow rugose ridge, and transverse narrow smooth tract. Lateral plate projecting anteriorly below antennal peduncle, its rather angular anterior tip bearing minute spine in line with base of eye; strongly rugose posterior part separated from somewhat less strongly rugose anterior part surrounded by impressed groove running submarginal to anteroventral aspect, then sweeping posterodorsally and recurving

anteriorly below line of rugae bordering lateral suture to point behind anterior tip.

Abdomen (Fig. 5*a*) unarmed but deeply sculptured; transverse ridges of segments 2–4 lightly rugose centrally but more strongly so laterally; segments 5 and 6 punctate, lightly rugose laterally. Telson (Fig. 2*i*) composed of 8 plates, length-width ratio 0.85, midlateral plates slightly convex on proximolateral margin.

Eyes (Figs. 5*a–b*) prominent; well exposed; smoothly ovate cornea cupped within broad based, fixed ocular peduncle bearing small anteromesial rugose patch but no spine; small, subtriangular plate posterolaterally adjacent to eye and anterior to frontal margin.

Basal article of antennular peduncle with distal margin irregularly crenulate; crest of slender compound dorsolateral spines and stronger anterolateral spine flanked by inflated lateral surface with irregular, small spinules at periphery; mesiodistal spine obsolescent. Antennal peduncle with fixed basal article extended into fimbriate distal margin, flat ventral spine, and shorter crenulate lateral spine; succeeding articles short, second bearing stout compound lateral angle and small, simple, distomesial angle; third with acute mesiodorsal angle; fourth with scalloped distal margin.

Third maxilliped with ischium shorter than merus, bearing mesial crest armed with finely uniform, evenly spaced corneous tipped spines, an acute distodorsal angle, and subrectangular distoventral angle flanked laterally by obsolescent spine. Basis with 0 or 1 obsolescent spine in line with crest on ischium. Merus (Fig. 5*c*) with 3 strong spines on flexor margin; distal margin irregular; extensor margin broadly arched, bearing 4 obsolescent spines and a more prominent spine distally; ventral surface lightly rugose. Carpus, propodus, and dactyl folded on merus-ischium and about as long as those 2 articles together; dense setation on dorsal surface of each, and distally on flexor surface of propodus and dactyl. Sternite at base of third maxilliped (Fig. 5*d*) rather slender, anterior margin bilobed, mesial lobe surmounted by small spine.

Epipods present on coxae of pereopods 1–3. Pereopods missing.

Eggs few, large, principal axes measuring 1.3 × 1.9 mm.

Remarks.—The distinctiveness of *Munidopsis granosicorium* leads us to describe it as a new species even though it is represented by a single imperfect specimen. This species seems close to *M. follirostris* Khodkina, 1973, from off the Pacific coast of South America (30°13′9″S, 78°47′W, 1,280 m) in general features of the carapace, the abdomen and telson, and in the relatively large cornea; however, it differs in having the rostrum triangular rather than markedly constricted near the base, and the gastric region elevated in anterior profile rather than evenly rounded (see Khodkina 1973).

More distantly, presence of epipods on the chelipeds and first two ambulatory legs links the species to *M. rostrata* (A. Milne Edwards, 1880) and *M. spinosa* (A. Milne-Edwards, 1880), but lack of any spine on the gastric region of the carapace separates it from these 2 species. The rostrum also differs from that of *M. rostrata* in lacking distinct lateral teeth, and from that of *M. spinosa* in having some very small marginal spines or tubercles (see Chace 1942). The short, immovable, spineless eyestalks link the new species to *M. espinis* Benedict, 1902, but it differs from that species in the deeper sculpturing of the carapace and abdomen, and in the dense scattering of small rugae but lack of spines on the carapace, and in having the merus of the third maxilliped armed with 3 rather than 2 spines on the flexor surface. There is only one record of *M. spinosa* from the western Pacific, and *M. rostrata* is represented by records from a circumglobal band between lat. 40°N and 35°S (see Baba 1988).

Etymology.—The specific name is a noun in apposition from the Latin, "granosus", full of grains, and "corium", leather, for the pebble-grained surface of the carapace resembling Scotch grained leather.

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Catch Efficiencies of Purse and Beach Seines in Ivory Coast Lagoons

Emmanuel Charles-Dominique

ABSTRACT: Catch efficiencies of two commonly used fishing gears in Ivory Coast lagoons, purse seine and beach seine, were studied. Only fish larger than the 100% mesh retention size (L_{100}) were considered. Escapement was estimated from the retention rates of marked fish released within the closed seines in shallow waters. Simple and reliable upper estimates of the catch efficiency were provided by these retention rates, which ranged from 10% to 79% for the purse seine and from 35% to 53% for the beach seine depending on the species. The purse seine efficiency was estimated by performing 25 sets (one set covering 0.72 ha) inside the closed beach seine (covering 9.4 ha), on both marked and unmarked populations of the bagrid *Chrysichthys* spp. and the cichlid *Tilapia guineensis*. The efficiency was close to 15% for the species considered, but this estimate may be sensitive to experimental bias (marking and "enclosure" effects). Avoidance, calculated for the purse seine from escapement and efficiency, appears to be considerable. Comparison of the catch rates by the two gears showed interspecies selectivity ("species selectivity") and intraspecies selectivity ("size-selectivity", regardless of mesh size). An understanding of both types of selectivity appears to be essential for an interpretation of the catch rates.

Artisanal fisheries are well developed in Ivory Coast lagoons, yielding from 10,000 to 20,000 tons of commercially valuable fish per year. Various stock assessment programs have been initiated at the Abidjan C.R.O. (Centre de Recherches Océanographiques) for fisheries management purposes during the last few years, but more direct methods of estimating fish abundance from catch rates are needed. The catch rates, which can be considered as relative abundance indices, can be converted into absolute abundance measurements, if the efficiency of fishing gear is known or can be estimated (Beverton and Holt 1956). Unfortunately, this is always a difficult process because efficiency depends upon various factors such as the behavior of fish, the environmental conditions (depth, nature of the bottom, etc.), and the physical characteristics of each particular gear. Previous studies have mostly dealt with towed gears such as trawls and plankton nets (Barkley 1972; Kjelson and Colby 1977; Merdinyan et al. 1979). The efficiency of these gears appeared to be a function of the active avoidance rate by fish, and models can be designed to explain, at least partially, the process (Barkley 1964). Measures of gear efficiency have been based on the "swept-area method" (Beverton and Holt 1956). Mark-recapture experiments have been made in well-defined areas, and the recapture rate has been compared with the ratio between the area swept by the gear and the area where the marked fish have been distributed (Kuipers 1975; Loesch et al. 1976; Watson 1976; Kjelson and Johnson 1978). Unlike trawl nets, surrounding nets and beach seines have rarely been studied in terms of efficiency, except the Danish seine (Hemmings 1973), which can be compared with a beach seine. For the surrounding–type gears, there are two different phases: 1) the shooting of the net, during which active avoidance takes place, and 2) the hauling of the net on board once the circle is closed, during which escapement can occur.

In this report, an experiment, based on an estimation of catchability according to the areas swept by the gears, in conjunction with a mark-recapture procedure, is described. This study was designed to better understanding multi-species catch-rates and to provide estimations of catchability for stock assessment.

MATERIAL AND METHODS

The two main fishing methods used in the Ivory Coast lagoons are the beach seine without a bag for shallow waters (about 1,200 m long) and the purse seine for depths of 2 m or more (ranging from 300 to 500 m long). Both gears reach the bottom and catch pelagic species as

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well as demersal species (Durand et al. 1978; Charles-Dominique 1983).

In this experiment, the purse seine was 305 m long on the lead-line and 14 m deep; the net was in excellent condition. The beach seine was 1,100 m long and 8 m deep; although the net was carefully checked, a few holes may have been overlooked owing to its very large size. The mesh size for both seines was 14 mm (bar measure).

Catchability (q) is the probability of capturing one fish from the standing stock by one unit of effort ($q = C/N$, where C is the catch in number per unit of effort and N the total standing stock). It may be divided into three elements (Laurec and Le Guen 1981): 1) overall accessibility (p_A), the probability of the presence of one fish in the fishing area A; 2) local accessibility (p_a), the probability of the presence of one fish in the area a that has been swept by the gear in one fishing operation; and 3) efficiency (e), the ratio of the number of fish caught to the number of vulnerable fish that were present in the area swept in one set (see Figure 1). Thus,

$$q = p_A \cdot p_a \cdot e \qquad (1)$$

In shallow waters, where the net reaches the bottom, the efficiency can be broken down into a product of three retention rates, corresponding to three successive phases: 1) avoidance (u), beginning with the net-shooting and ending with its closing; 2) escapement through the mesh (v), occurring if the fish size is less than L_{100} (the size at which 100% of fish are retained by the mesh); and 3) other forms of escapement (w), i.e., jumping over the net, burrowing or slipping through holes in the net or under the lead-line.

This catch efficiency can be written as follows:

$$e = u \cdot v \cdot w \text{ (purse seine)} \qquad (2)$$

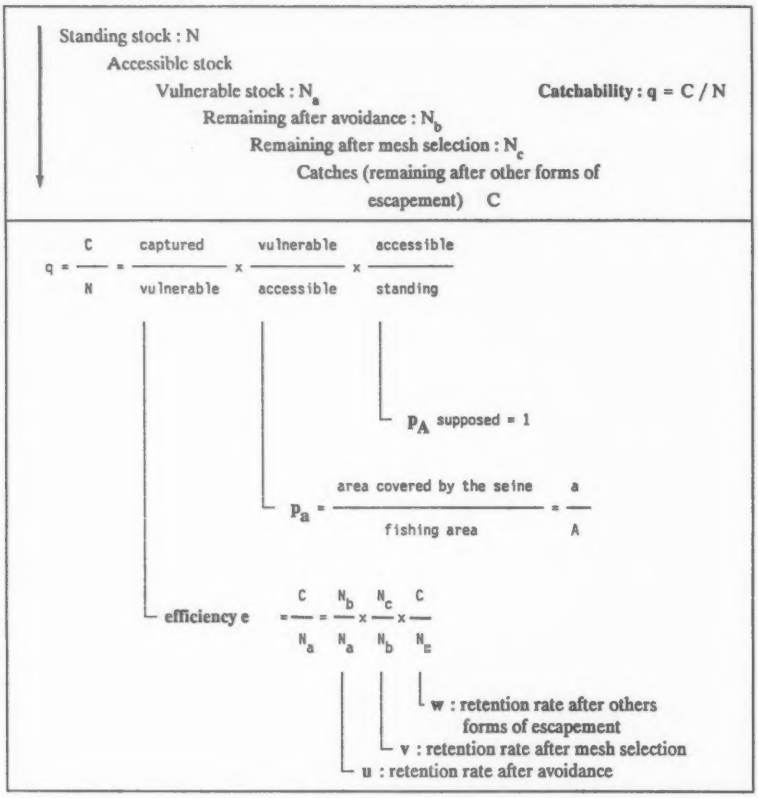
Standing stock : N
Accessible stock
Vulnerable stock : N_a
Catchability : q = C / N
Remaining after avoidance : N_b
Remaining after mesh selection : N_c
Catches (remaining after other forms of escapement) C
$q = \frac{C}{N} = \frac{\text{captured}}{\text{vulnerable}} \times \frac{\text{vulnerable}}{\text{accessible}} \times \frac{\text{accessible}}{\text{standing}}$
p_A supposed = 1
$p_a = \frac{\text{area covered by the seine}}{\text{fishing area}} = \frac{a}{A}$
efficiency e $= \frac{C}{N_a} = \frac{N_b}{N_a} \times \frac{N_c}{N_b} \times \frac{C}{N_c}$
w : retention rate after others forms of escapement
v : retention rate after mesh selection
u : retention rate after avoidance

FIGURE 1.—Schematic representation of the catchability parameters for a seine in shallow waters and the catchability equation that comprises these parameters.

$$E = U \cdot V \cdot W \text{ (beach seine)} \qquad (3)$$

where capital letters refer to the beach seine and small letters to the purse seine (Table 1).

TABLE 1.—Summary of the methods used in this paper to estimate the parameters of the catchability, as defined in the text and on figure 1. Small letters refer to the purse seine and capital letters to the beach seine.

Parameters	Purse	Beach sine
Retention rate after escapement through mesh	v = for fishes greater than L_{100}, 100% mesh retention size	V = 1 (idem)
Retention rate after other forms of escapement	w = 15 independent mark-recapture estimates	W = 2 measures (W_1, W_2), 5 replica
Catchability	g = 5 measures using two methods (from captures and from recaptures)	—
Efficiency	$e = q \cdot a/A$ a = area covered by the purse seine (0.72 ha) A = area covered by the beach seine (9.4 ha)	E = W
Avoidance	$u = e/w$	supposed negligible

Two independent experiments were designed 1) to estimate the purse seine retention rate and 2) to estimate both the beach seine retention rate and the purse seine efficiency.

To estimate the purse seine retention rate, 15 mark-recapture experiments ($i = 1 \ldots 15$) were conducted in the open lagoon.[1]

Marking was done without anaesthetic by clipping either the superior lobe of the caudal fin, the right or left pelvic fin, or the adipose fin. Fish were stored in 1 m^3 floating cages with up to 100 fish per cage. The minimum size of the marked fish (mm) was greater than the L_{100}.[2]

At each experiment i, m_i fish were marked and released within the "closed" purse seine (i.e., when the two ends of the seine are joined together before pursing). At the end of the fishing operation, the species and sizes of the recaptured fish (r_i) were noted, and the retention rate ($w_i = r_i/m_i$) was calculated for each set. The weighted average (w) and variance ($v(w)$) were then calculated (Table 2).

$$w = \frac{\Sigma r_i}{\Sigma m_i}$$

[1]The experience was conducted in the Aby lagoon, one of the largest lagoons of the Ivory Coast (424 km^2), situated on the southwest of the country.

[2]Fish were larger than 9 cm (*Chrysichthys* spp.) or 10 cm (*Tilapia guineensis*). See footnote 3: Cantrelle et. al. (1983).

TABLE 2.—Estimation of the purse seine retention rate (w) from releasing m fish within the closed purse seine and recapturing them (r). C.V. is the coefficient of variation in percentage.

		Purse seine mark-recapture experiments																
Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	w	C.V.
Tilapia guineensis	*m*	20	3	12	15	2	34	45	1	18	23	9	16	5	28	21	0.544	27
	r	11	2	10	9	1	16	17	1	10	12	8	10	5	12	13		
Chrysichthys auratus	*m*	1	1		6		6	2	30		14	20	13	2	3	23	0.711	34
	r	0	0		6		3	1	29		9	13	11	2	3	9		
Chrysichthys maurus	*m*	19	40		26	25	27	41	62	14	67	2	7	32	5	38	0.760	21
	r	13	37		19	13	24	38	30	8	57	2	6	24	5	32		
Chrysichthys nigrodigitatus	*m*	2			18	8	1	10					2			2	0.581	33
	r	1			11	6	1	3					1			2		
Hemichromis fasciatus	*m*	1	3	2						9	2	2	1	17	6	4	0.787	32
	r	1	2	2						5	2	2	1	17	4	1		
Tylochromis jentinki	*m*					6		1	1	3		1	1			4	0.471	73
	r					3		0	0	0		1	1			3		
Gerres spp.	*m*											6	51	35	41		0.699	25
	r											4	47	19	23			
Callinectes amnicola	*m*				6	4	13	6	6	9	4	10	8		5		0.099	95
	r				1	1	2	1	1	0	1	0	0		0			

$$v(w) = \frac{\Sigma(r_i^2/m_i)}{\Sigma m_i} - \left[\frac{\Sigma r_i}{\Sigma m_i}\right]^2$$

In the second experiment, the beach seine was set in a shallow area of a lagoon where the average depth was 3 m. Fish were marked with a type-1 mark (M_1 fish) at the beginning of the experiment and released into the closed beach seine. A 30 min delay allowed the fish to disperse in the enclosure. Five successive purse seine sets were made randomly within the beach seine. Each set lasted about 22 minutes (the net was closed after about 3 minutes; the rings were placed on-board after about 9 minutes).

Species and size of captures and recaptures were recorded for each purse seine set; the unmarked fish were marked with a type-2 mark and stored in the floating cages. After the fifth purse seine set, the marked fish in good condition were released (M_2 fish). The retrieval of the beach seine took 6 hours. Species and size of the captures and recaptures (both M_1 and M_2 types) were recorded (Table 3). The experiment was repeated five times.

In this experiment, one should note that the storing period differed for marked fish: the marked-1 fish, captured the day before, were held captive approximately 15 hours, while the marked-2 fish on average were retained only 1 hour in the cages. Based on an aerial observation, the shapes of the seines were almost circular, although the beach seine was in some cases distorted by tidal currents; however, it was assumed that the nets were perfect circles (purse seine area 0.72 ha, beach seine area 9.4 ha).

Two retention rates by the beach seine (W_1 and W_2) were calculated for the whole experiment:

$$W_1 = R_1(M_1 - (r_{11} + r_{12} + r_{13} + r_{14} + r_{15}))$$

and for the second period of the experiment (beginning after the fifth purse seine set):

$$W_2 = R_2/M_2.$$

W_2 and W_2 correspond to fish that have stayed an average of 8½ hours and 6 hours in the enclosure respectively; thus, W_1 was expected to be lower than or equal to W_2. The difference between W_1 and W_2 was tested with a χ^2 test at the 0.05 level (Dagnélie 1975, p. 88). If W_1 and W_2 did not differ significantly, escapement was assumed not to have occurred during the purse seine fishing period. The mean retention rate (W) was calculated:

$$W = (R_1 + R_2)/(M_1 - (r_{11} + r_{12} + r_{13} + r_{14} + r_{15}) + M_2).$$

Assuming that the fish were equally available inside the enclosure, the overall accessibility (p_A) is 1 and the expectancy of the local accessibility (p_a) is equal to the ratio of the areas cov-

TABLE 3.—Experimental scheme used to measure the purse seine efficiency and the beach seine retention rate: a large beach seine reaching the bottom is set and closed over a shallow area, making a circular enclosure. M_1 fishes are marked and released within it at time 0, and a 30 min delay allows them to disperse. Five purse seine sets are then successively made within the enclosure. At every set i, the catches c_i and recaptures r_{1i} are recorded. The standing stock within the enclosure before set i is noted N_i. The unmarked fishes caught with the purse seine are marked with a type-2 mark (m_{2i}) and stored, then are released together after the fifth purse seine set (M_2). The beach seine is then retrieved and catches (C) and recaptures of both type-1 (M_1) and type-2 (M_2) are recorded.

Operations		Beach seine closed	Five purse seine sets (in hours elapsed) 0.5	1	1.5	2	2.5	Beach seine retrieved	Beach seine catches
Standing stock			N_1	N_2	N_3	N_4	N_5	N_6	
Releasing	mark-1	M_1							
Captures			c_1	c_2	c_3	c_4	c_5		C
Recaptures	mark-1		r_{11}	r_{12}	r_{13}	r_{14}	r_{15}		R_1
Marking	mark-2		m_{21}	m_{22}	m_{23}	m_{24}	m_{25}		
Releasing	mark-2							M_2	
Recaptures	mark-2								R_2

ered by the gears, $p_a = a/A$; therefore, according to Equation (1), $e = q \cdot A/a$.

Catchability q was estimated by using two partially independent methods (see notations on Table 1). In the first method (estimation "from captures"), catchability was estimated for each purse seining operation by the equation: $q_i = c_i/N_i$ ($i = 1...5$), where c_i represents captures at set i and N_i, the standing stock in the enclosure just before set i. When escapement did not occur during the first period ($W_1 = W_2$), the standing stock after last purse seine set (N_6) was estimated by the ratio of the beach seine captures (C) to the retention rate W. The previous values of N_i were then calculated backward ($N_i = N_{i=1} + c_i$, $i = 5...1$), and the q_i values follow.

In the second method (estimation "from recaptures"), catchability was estimated from the recaptures of marked-1 fish only when escapement did not occur during the first period ($W_1 = W_2$). In this case, $q_i = r_{1i}/M_{1i}$, where M_{1i} is the standing stock of marked-1 fish just before the set i. M_{1i} was calculated by successive subtraction of type-1 recaptures ($M_{1,i1} = M_{1i} = r_{1i}$).

The two methods of measuring q were compared using a distribution-free test (Wilcoxon's signed rank test, see Dagnélie 1975), which applies to paired data samples. The experimental design described above is summarized in Table 3.

Both methods rely on some underlying assumptions: A) no mortality of marked fish occurs; B) marked and unmarked fish have the same probability of escaping from the enclosure; C) the efficiency of the purse seine is equal for marked and unmarked fish; and D) all fish present in the enclosure have an equal probability of being caught. The method from captures relies on assumptions A), C), and D); the method from recaptures relies on A), B), and D).

RESULTS

Tagging and Holding Tolerance

No mortality of marked fish was observed during our experiment. This included the holding period in the floating cages as well as the fishing period (no dead marked fish were recovered in the seines). During the preliminary tests, however, marked fish of less robust species (*Ethmalosa fimbriata* and *Eucinostomus melanopterus*) were found dead in both the cages and the fishing nets.

Retention Rates

Purse seine captures and recaptures observed in the 15 independent mark-recapture experiments are listed in Table 2. The mean retention rates and the coefficient of variation were calculated for seven fish species and for the portunid crab *Callinectes amnicola*. The retention rate ranged from 0.47 to 0.79 for fish and was 0.10 for *C. amnicola*, which escaped in large numbers probably by burying itself. No fish were observed jumping over the purse seine net. Therefore, escapement appeared to be due to fish going under the lead-line.

Retention rates were estimated by size group for the two principal species, *Tilapia guineensis* and *Chrysichthys* spp. (grouping the three species, *C. maurus*, *C. auratus*, and *C. nigrodigitatus*). No difference was found between the size groups using a one-way analysis of variance by ranks (Kruskall-Wallis test, see Table 5).

The beach seine retention rates, W_1 and W_2, were calculated and their equality tested for the two principal species listed above (Table 4). For *Chrysichthys* spp., W_1 was always less than or equal to W_2. The mean retention rate (W) was 0.53. No size effect was found in the analysis of variance by size group (Table 5).

For *T. guineensis*, W_1 was less than or equal to W_2 in only two experiments. The mean retention rate was 0.35. In the three other experiments, the unexpected result of W_1 being greater than W_2 was found. This point will be discussed later. Again, no size effect was noticed (Table 5).

TABLE 4.—Estimation of the beach seine retention rates W_1 and W_2 (number of recaptured over number of released fish). If W_1 and W_2 do not differ significantly in one experiment (χ^2 test for the difference of two proportions, $P = 0.05$), the mean value W is then calculated. Parentheses mean a departure from the limit of application conditions of the test.

Retention rates	Capture dates (Oct. 1984) 8	9	12	13	16	Mean
Chrysichthys spp.						
W_1	7/15	57/78	28/107	78/141	31/106	
W_2	21/36	9/13	16/27	17/27	3/11	
χ^2	0.58	(0.36)	11.5	0.41	(0.13)	
W	0.55	0.73		0.57	0.29	0.53
Tilapia guineensis						
W_1	45/102	24/50	19/26	19/27	14/53	
W_2	38/90	28/92	27/102	13/36	8/27	
χ^2	0.07	4.31	19.5	7.2	0.09	
W	0.43				0.28	0.35

TABLE 5.—Comparison of the retention rates of purse seine (W) and beach seine (W_1 and W_2), calculated by size group: one-way analysis of variance by ranks (Kruskall-Wallis test). Critical value of $\chi^2_{0.95}$ is 7.81. M = mean, C.V. = coefficient of variation.

Purse seine					
Chrysichthys spp.					
Size	10–12 cm	13–15 cm	16–18 cm	>19 cm	χ^2_{obs}
W: M	0.725	0.776	0.686	0.622	2.21
C.V.	17	19	36	38	
Tilapia guineensis					
Size	8–11 cm	12–15 cm	16–19 cm	>20 cm	χ^2_{obs}
W: M	0.506	0.495	0.488	0.483	0.48
C.V.	50	43	68	49	
Beach seine					
Chrysichthys spp.					
Size	10–12 cm	13–15 cm	16–18 cm	>19 cm	χ^2_{obs}
W_1: M	0.563	0.476	0.386	0.377	0.75
C.V.	35	43	41	34	
W_2: M	0.565	0.632	0.600	0.250	0.40
C.V.	25	17	37	58	
Tilapia guineensis					
Size	8–11 cm	12–15 cm	16–19 cm	>20 cm	χ^2_{obs}
W_1: M	0.596	0.432	0.511	0.400	0.48
C.V.	35	23	66	47	
W_2: M	0.356	0.295	0.316	0.375	5.99
C.V.	38	25	67	111	

Catchability and Efficiency of the Purse Seine

The catchability equivalent to a purse seine set was estimated using both methods from captures (Table 6) and recaptures (Table 7). The mean and the standard deviation were then calculated.

For *Chrysichthys* spp., using the method from captures, q_c equaled 2.35% (SD = 5.38), and using the method from recaptures, q_r equaled 0.97% (SD = 2.03). Most of the variability of the q_c values comes from one set (#3, Date 13), where one quarter of the fish were caught. We tested the two q measures obtained for this set (24.2, 6.85) as outliers in their respective series (Dagnélie 1975, p. 34). With this procedure, the value to be tested was initially removed from the data, and a new mean and standard deviation were calculated (q_c' = 1.20, SD = 1.63). A Student's t statistic was then calculated (15.3 and 4.4 respectively) and compared with the 5% critical value $t_{0.05}$ = 3.6. This allowed us to discard the data from set #3. After removal of the outlier set, the difference between the two estimations of q, tested using the Wilcoxon's signed rank test, was not significant at the 0.05 level. Thus, the 39 measures of q were pooled for the calculation of the mean (q = 0.93) and SD = 1.58. The efficiency was then calculated using Equation 1 to be 12% ($e = 0.93 \cdot 9.4/0.72$).

For *T. guineensis*, the two catchability estimation methods yielded the following results: using the method from captures (Table 6), the mean, noted q_c equaled 3.54 (SD = 1.70) and from recaptures (Table 7), the mean, noted q_r, equaled 1.39 (SD = 1.44).

We compared the two samples (Wilcoxon's rank test) and found a highly significant difference (P = 0.01). The q_r value was considered to be more reasonable and the reasons will be discussed later. The efficiency follows was then calculated to be 18% ($1.39 \cdot 9.4/0.72$).

Avoidance of the Purse Seine

The avoidance rate (u) was estimated using Equation (2), $e = u \cdot v \cdot w$ (pooled mean from Table 2), knowing e, w, and with v being equal to 1 in our experimental conditions. For *Chrysichthys* spp., e = 0.12 and w = 0.73, thus, $u = e/w$ = 0.16. Thus active avoidance rate appears to be the main factor in the efficiency. For *T. guineensis*, the q_r estimation from recaptures

TABLE 6.—Estimation of the catchability relative to the purse seine by the method "from captures" (c_i = purse seine captures; N_i = standing stock; q_i = catchability %; C = beach seine catches; W = beach seine retention rate).

Dates (Oct. 1984)		Set numbers 1	2	3	4	5	6	C,W
Chrysichthys spp.								
8	c_i	4	1	13	6	15		149
	N_i	310	306	305	292	286	271	0.55
	q_i	1.29	0.33	4.26	2.05	5.24		
9	c_i	0	10	0	0	0		1,031
	N_i	1,367	1,367	1,357	1,357	1,357	1,357	0.76
	q_i	0	0.73	0	0	0		
13	c_i	3	0	32	4	1		56
	N_i	135	132	132	100	96	95	0.59
	q_i	2.22	0	24.2	4.00	1.04		
16	c_i	0	2	1	2	5		202
	N_i	641	641	639	638	636	631	0.32
	q_i	0	0.31	0.16	0.31	0.79		
Tilapia guineensis								
8	c_i	16	17	9	26	28		165
	N_i	480	464	447	438	412	384	0.43
	q_i	3.33	3.66	2.01	5.94	6.80		
16	c_i	3	5	9	5	3		47
	N_i	193	190	185	176	171	168	0.28
	q_i	1.55	2.63	4.86	2.84	1.75		

TABLE 7.—Estimation of the catchability by the purse seine by the method "from recaptures" (m_i = marked fish; r_i = recaptured fish; q_i = catchability, as a percentage).

Dates (Oct. 1984)		Set numbers 1	2	3	4	5
Chrysichthys spp.						
8	r_i	0	0	0	0	1
	m_i	16	16	16	16	16
	q_i	0	0	0	0	6.25
9	r_i	0	0	0	0	0
	m_i	78	78	78	78	78
	q_i	0	0	0	0	0
13	r_i	0	0	10	3	0
	m_i	146	146	146	136	133
	q_i	0	0	6.85	2.21	0.00
16	r_i	0	0	1	1	2
	m_i	100	100	99	98	97
	q_i	0	0	1.01	1.02	2.06
Tilapia guineensis						
8	r_i	1	5	1	1	3
	m_i	133	112	107	106	105
	q_i	0.88	4.46	0.93	0.94	2.89
16	r_i	1	0	0	1	0
	m_i	53	52	52	52	51
	q_i	1.89	0	0	1.92	0

yielded $e_r = 0.18$ and $w = 0.54$ (Table 2), thus, $u_r = 0.33$. According to these results, the purse seine seems comparably efficient for both species (12% and 18%), but the avoidance and the escapement rates are very different.

Species and Size Selectivity

The total catches by the purse seine (25 sets) and by the beach seine (5 sets) are summed in Table 8, along with the ratio of these values. Important difference appear between the ratios for the 16 species listed. They range between 0.003 and 0.17; this will be termed "species selectivity".

The same ratio was also computed by size group for seven species and analyzed using a Kruskall-Wallis one-way analysis of variance (Table 9). A large size effect, termed here "size selectivity", appears for *T. guineensis* and is likely for *Gerres nigri*, but is not significant for the other species.

TABLE 8.—Total catches in number by purse seine (PS) and beach seine (BS) during the whole experiment. The mean ratio of catches per set by both gears is calculated with the coefficient of variation (C.V.) expressed as a percentage.

Species	PS	BS	Ratio	C.V.
Gerres nigri	167	8,591	0.0039	130
Pomadasys jubelini	6	143	0.0084	101
Tylochromis jentinki	22	366	0.0120	32
Chrysichthys auratus	139	2,232	0.0125	127
Chrysichthys maurus	26	384	0.0135	120
Chrysichthys nigrodigitatus	9	96	0.0187	127
Caranx hippos	2	17	0.0235	132
Elops lacerta	135	1,049	0.0257	39
Arius latiscutatus	6	32	0.0375	173
Ethmalosa fimbriata	1,958	8,816	0.0444	37
Trachinotus teraia	11	44	0.0500	148
Sarotherodon melanotheron	27	81	0.0667	156
Callinectes amnicola	96	137	0.1401	261
Citharichthys stampflii	61	75	0.1627	145
Tilapia guineensis	362	437	0.1657	18
Penaeus notialis	1,234	32	7.7125	92
Total	2,973	22,963	0.0259	

DISCUSSION

The validity of the different results depends to a large extent on the robustness to departures from the underlying assumptions: no marking and holding stress, no mortalities, and no enclosure effect (e.g., accessible stock may differ from the standing stock if fish are crowded along the enclosure).

Escapement

For the *Chrysichthys* spp., the estimates of the retention rates are consistent with estimates of catchability and seem valid. On the other hand, for *T. guineensis*, the retention rates lead to unexpected results on three occasions ($W_1 > W_2$, Table 4). Marked-1 fishes escaped less than

TABLE 9.—Comparison of the catches per set by both gears, by size group, using a one-way analysis of variance by ranks (Kruskall-Wallis test). Critical value of $\chi^2_{0.95}$ is 7.81.

Species		Size group 1	2	3	4	χ^2_{obs}
Tilapia guineensis	R	1.127	0.804	0.556	0.154	12.78
	C.V.	35	23	48	32	
Gerres nigri	R	0.012	0.023	0.036	0.102	6.15
	C.V.	105	130	99	54	
Elops lacerta	R	0.144	0.092	0.113	0.244	0.09
	C.V.	18	181	87	32	
Ethmalosa fimbriata	R	0.202	0.454	0.376	1.091	2.38
	C.V.	58	1,289	166	201	
Chrysichthys auratus	R	0.065	0.065	0.030	0.077	3.44
	C.V.	130	164	181	235	
Chrysichthys maurus	R	0.162	0.040	0.029	0	5.82
	C.V.	175	294	84		
Chrysichthys nigrodigitatus	R	0.087	0	0.187	0.080	2.30
	C.V.	57		140	163	

marked-2 ones, even though they spent more time inside the beach seine and thus had more opportunities to escape. To explain this result, consider how the two sets of marked fish might have differed: 1) by sampled sizes, 2) by the type of mark, and 3) by the duration of the holding period. Sampling of sizes does not need to be examined because there was no significant correlation between the size and the retention rate. The type of mark itself did not seem likely to influence the fish behavior. However, the duration of the holding period was much longer for marked-1 fish, increasing the opportunities to escape and thus to overestimate W_1. For *T. guineensis*, the two q estimations (Tables 6, 7) differed to a large degree. This was probably due to the stress on marked-1 fish, leading to an overestimation of W_1, and thus to an overestimation of the catchability (q_c) calculated by the capture method. The W value that would produce a catchability estimate of $q_r = 1.39\%$ has been calculated iteratively and equals 14%. This retention rate is very low but is consistent with the known behavior of this cichlid species, which escapes from beach seines by slipping under the lead line and by jumping over the net (to recover the jumping fish, local fishermen often place small canoes equipped with net curtains along the seine).

In any case, a retention rate estimated with a marking procedure is greater or equal to the actual efficiency and can be used as an upper estimate of the efficiency. For example, efficiency of the purse seine for the crab *C. amnicola* is smaller than the observed 10% retention rate (Table 3).

The comparison of the retention rates for both seines indicates that the purse seine is more efficient in limiting escapement than the beach seine. This can be explained to some extent by the difference in the duration of the sets (22 minutes versus 6 hours). The rigging of the gears may also have an influence; the purse seine lead-line hugs the bottom, owing to the drag and weight of the rings, more efficiently than the beach seine; noise and vibrations in the ropes also generally keep the fish away from the net (Hemmings 1967). Therefore, pursing is more efficient than the manual closing of the beach seine. The better efficiency of the purse seine should, however, not be generalized because the efficiency of a particular gear may be influenced by subtle differences of rigging (MacMullen 1981). We did observe during another experiment[3] some important differences in the efficiencies of two apparently similar purse seines, probably resulting from a slight difference in lead-line weights.

Species and Size Selectivity

Other robust results came from a comparison of the catch rates of the two gears in terms of species relative abundance (species selectivity) and size distribution (size selectivity).

Species selectivity is due to differences between the efficiencies, which depend upon complex interactions between the gears and the behavior of the species. In this experiment, an additional "enclosure effect" can happen if all fish are not equally available. For instance, by crowding along the net, the fish become inaccessible to the purse seine (p_A, the overall accessibility is then less than 1).

The ratio of catch rates by the two gears, calculated in Table 8, can be compared to the theoretical value that would be obtained if both gears were equally efficient, and if the avoidance rate for beach seine was negligible. This can be assumed as a first approximation since the net is very large (1,100 m) and fairly silent (no engine was used in the boat).

From the formulas given above (see methods: estimation from captures):

$$c_i = \frac{q \cdot C}{W} \cdot \frac{1}{(1 = q)^{6-i}} \qquad \text{and } r = \frac{q}{W} \cdot \alpha,$$

$$\text{with } \alpha = \frac{1}{(1 - q)} + \frac{1}{(1 - q)^2} + \ldots + \frac{1}{(1 + q)^5}$$

since $q = p_a \cdot e$, then $r = p_a \cdot (e/W) \cdot \alpha$.

The parameter r appears to be roughly proportional to e/W, α being a correction factor accounting for the successive catches in the enclosure. The parameter α, depending on the value of e, which varies between 0 and 1, is in the interval (1–1.276). If the efficiencies of the two gears are equal ($e = E$ or $e = W$, since U is assumed to be equal to 1), r is in the interval $[p_a - 1.276 \cdot p_a]$, that is [0.076–0.097]). In Table 8, r is smaller than 0.076 for most fish species, indicating lower efficiency of the purse seine. On the contrary,

[3]Cantrelle, I., E. Charles-Dominique, Y. N. N'Goran, and J. Quensière. 1983. Etude expérimentale de la sélectivité de deux sennes tournantes et coulissantes (maillage 25 mm et maillage mixte 14–2" mm) en lagune Aby (Côte d'Ivoire). Unpubl. rep., 36 p. Cent. Rech. Océanogr, Abidjan.

the purse seine is more efficient for the burrowing species (*Callinectes* spp., *Citharichthys stampflii*, *Penaeus notialis*) and for *T. guineensis*.

Size selectivity appears for two species (*T. guineensis* and *G. nigri*) when the ratio of catches is calculated by size group (Table 9). As it has been shown above for the marked species, the size composition of fishes in the enclosure during the experiment does not differ from that of the final catches of the beach seine. Two factors remain explaining this size selectivity: 1) a size selective accessibility within the enclosure and 2) a size selective catchability by the purse seine. The first factor is impossible to assess. The second one may happen with active gear, like the seines. Larger individuals may be better able to avoid capture because of their higher maximum swimming speed (Bainbridge 1958; Blaxter 1967). This type of size selectivity has been shown in sampling plankton larvae with an experimental active gear (Murphy and Clutter 1972), and may here explain the decrease in the ratio of the catch rates with size in *T. guineensis*.

In *G. nigri*, the selectivity is reversed, small sizes being underrepresented in the purse seine catches. This point seems difficult to interpret, and probably complex mechanisms are involved: enclosure effect (size-dependent accessibility) and size dependent catchability owing to complex behavior. Some descriptions of complex behavior of fish during a fishing operation are given in the literature. For trawlers and Danish seines, the flight is triggered by a stimulus, mainly visual, from the moving gear at a certain distance (MacMullen 1981). Different species react differently; some demersal species jump perpendicularly, while others jump in random directions (Hemmings 1967). Anchovies surrounded by a purse seine tend to move into deeper waters (Inoue and Ayodhyoa 1967).

Efficiency

For the results of the efficiency measurement to be valid, all of the assumptions must be met. Consequently, efficiency estimates may not be completely reliable.

Efficiency of the purse seine for fishes larger than L_{100} is very low according to our results (*Chrysichthys* spp., 12% and *T. guineensis*, 18%). Actually, purse seining is an efficient technique when based on spotting and surrounding pelagic fish schools. However, it probably becomes very inefficient for "blind" fishing of demersal species, as was done in this experiment and as is often practiced in Ivory Coast lagoon fisheries. The main cause of this inefficiency is most likely the avoidance during the surrounding phase of the operation.

The efficiency of a large, nonmotorized beach seine, reaching the ground in shallow waters, depends mostly on a low escapement rate after closing the net. Estimation of the escapement rate by mark-recapture can thus provide a simple and reliable upper estimate of efficiency. However, it is important to stress that a general application of such values to the entire fishery is not possible unless the variability of gears and fishing grounds is considered.

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Otoconia From Four New Zealand Chimaeriformes

K. P. Mulligan, R. W. Gauldie, and R. Thomson

ABSTRACT: A scanning electron microscopy and x-ray diffraction investigation of chimaeriform otoliths shows densely packed and strongly bound aggregations of otoconia in the form of aragonitic spherulites. Characteristic sizes, shapes, and surface features are described for each of the four species investigated. Otoconial diameters differ among species, but the chimaeras are nonetheless a uniform group in terms of otoconia type and otolith shape.

Members of the Class Chondrichthyes (elasmobranchs and Chimaeriformes) are known to have otoliths composed of otoconia bound in a protein matrix (Stewart 1903; Iseltöger 1941; Carlström 1963; Barber and Emerson 1980). The use of the term otolith in reference to chondrichthyan fish requires some clarification. There are difficulties in establishing chemical or crystalline homologies between aggregated otoconia and otoliths proper as they occur in teleosts. However, they are similar in being semirigid or rigid structures supported on a hair cell pad and involved in sound transduction in both elasmobranchs and teleosts (Popper and Fay 1977; Fay 1983). When homologies are established, a general term for a crystalline, calcium carbonate structure associated with sound transduction may appear, but until then we will persist in using the term otolith in a more general sense than its derivation implies.

Studies on the otolith of the chimaera *Callorhynchus milii* (Callorhynchidae), which is found in inshore waters of New Zealand, showed that it was composed of fused spherulitic otoconia (Gauldie et al. 1987). Spherulite otoconia were one of three differing forms of otoconia, which were found in the Australian lungfish *Neoceratodus forsteri* (Gauldie et al. 1986a), and were similar to the type of free otoconia found in conjunction with the otoliths of some teleosts (Dale 1976; Gauldie et al. 1986b) and described in some shark species (Carlström 1963).

Spherulitic otoconia fused into otoliths have also been described in humans, occurring in association with hereditary deafness (Johnsson et al. 1981). Humans normally have only calcitic otoconia similar to those occurring in the lungfish, but apparently there are still human genes that will code for the spherulitic otoconia. It is tempting to see the widespread distribution of spherulitic otoconia as an indication that they are the most primitive kind of crystalline calcium carbonate secreted by the vertebrate ear. There are strong similarities between the shapes and anatomical arrangement of the otoliths in the chimaera *C. millii* and the lungfish *N. forsteri*, as well as in some of their constituent otoconia. These observations support the suggestion (Patterson 1965; Romer 1968) that the modern chimaeras might be descended from ptyctodont placoderms. Thus, apart from the issue of chimaera affinities within the elasmobranchs (Zangerl 1973), the spherulitic otoconia of the chimaeras may hold some clues to the fundamental mechanism of otolith deposition.

Several species of deep-water chimaeras occur in New Zealand's waters. Otolith form and structure from the two families Rhinochimaeridae (*Harriotta raleighana* and *Rhinochimaera* sp.) and Chimaeridae (*Hydrolagus novaezelandiae* and *Chimaera* sp.) are investigated in this paper.

MATERIALS AND METHODS

Three specimens of each species—*H. raleighana*, *Rhinochimaera* sp., *H. novaezelandiae*, and *Chimaera* sp.—were caught in a deep-water trawl survey of the Chatham Rise area, December 1985. Heads were placed in a 10% neutral buffered formalin solution for 24 hours and transferred to 70% isopropanol until dissection. The preservative solutions remained alkaline during storage time, but after more

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lengthy periods (more than 6 months), 70% isopropanol became weakly acidic with a pH of 6.5–6.7. All otic complexes were removed from heads within three weeks of initial fixation. Samples were then photographed with a Wild M400[1] photomicroscope before their otoliths were removed in preparation for scanning electron microscopy (SEM). Selected whole and fractured portions were then dehydrated in an ethanol series, mounted on stubs with a metallic cement, and sputter-coated with gold under five atmospheres of pressure before being viewed on a Philips 505 SEM.

Analyses of samples by x-ray diffraction were carried out on a Philips PW1279/PW1710 x-ray diffractometer. Operating conditions for the diffractometer were the following: 45 kV for the Cu tube; 40 mA for the automatic divergence slit; 0.1 mm for the receiving slit; 1° for the scatter slit; and a Ni filter. Goniometer speed was set at 3°2θ/min, and chart speed was set at 10 min/°2θ from 5 to 55°2θ. The error of estimated proportion of calcium carbonate morph (calcite, aragonite, and vaterite) was ±5%. Otoconial dimeters were directly measured from SEM photographs.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

The general shape and organization of the four chimaeriform otic complexes (including semicircular canals and otoliths) resembled the shape and organization of *C. milii* (Gauldie et al. 1987). Two otoliths occurred within a single sac, oriented at more or less right angles to each other, and presumably corresponded with the sagitta and astericus of teleosts. All of the otoliths described in this study were the sagittae.

The otoliths of the Chimaeriformes were solid masses of aggregated otoconia (Fig. 1A, B, C). Otoliths of *H. novaezelandiae* had densely packed central areas with looser aggregations of otoconia on the exterior surface (Fig. 1B). The matrix was less apparent in *H. raleighana*, and the otolith was characterized by many small otoconia (Fig. 1C), giving a loose granular appearance, while *Rhinochimaera* sp. otoliths (Fig. 2A) had closely packed arrays of otoconia. *Chimaera* sp. otoliths (Fig. 2B) were solidly packed with less cohesive matrix material visible.

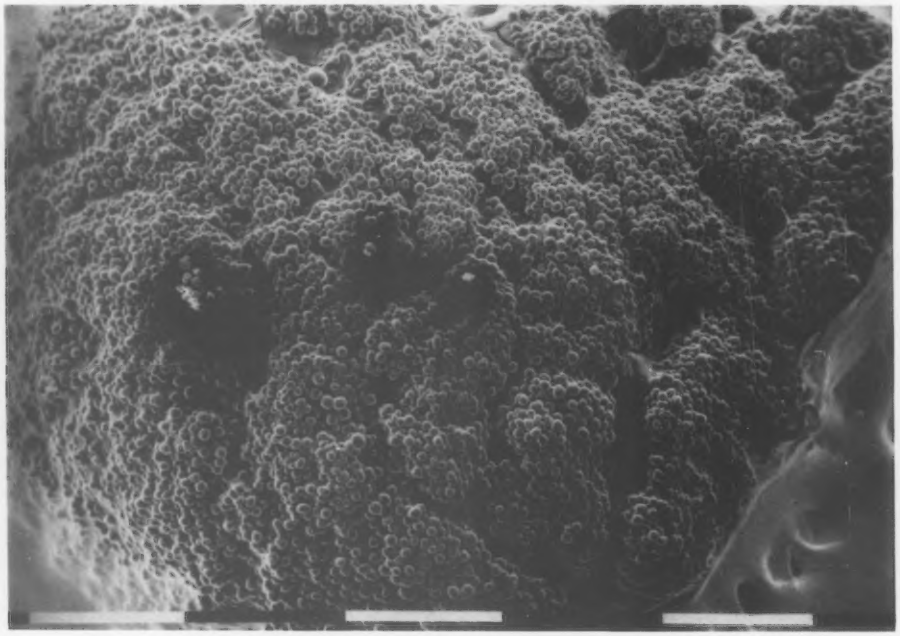


FIGURE 1A.—*Rhinochimaera* sp. otolith. Bar = 1 mm.

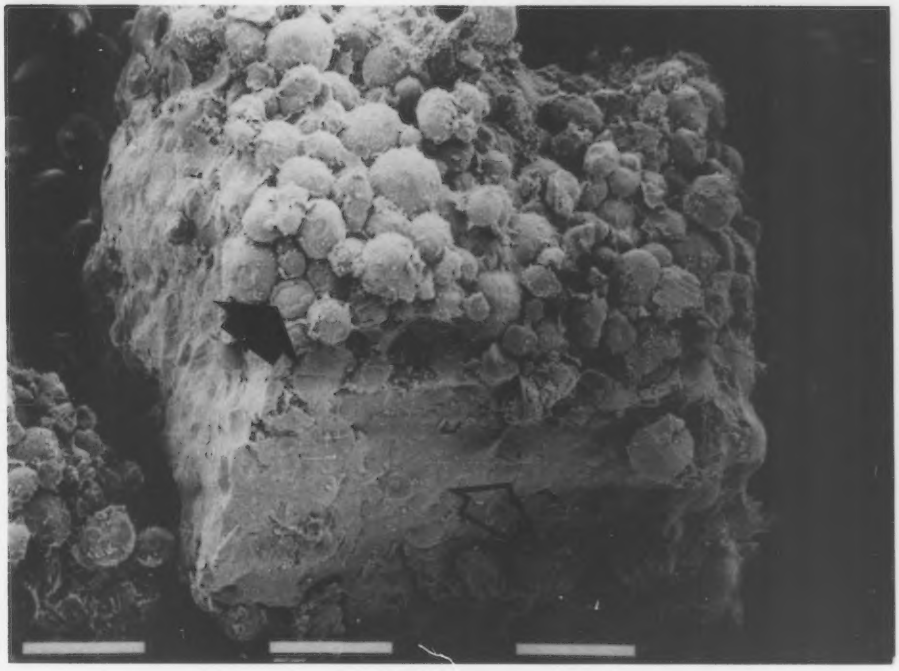
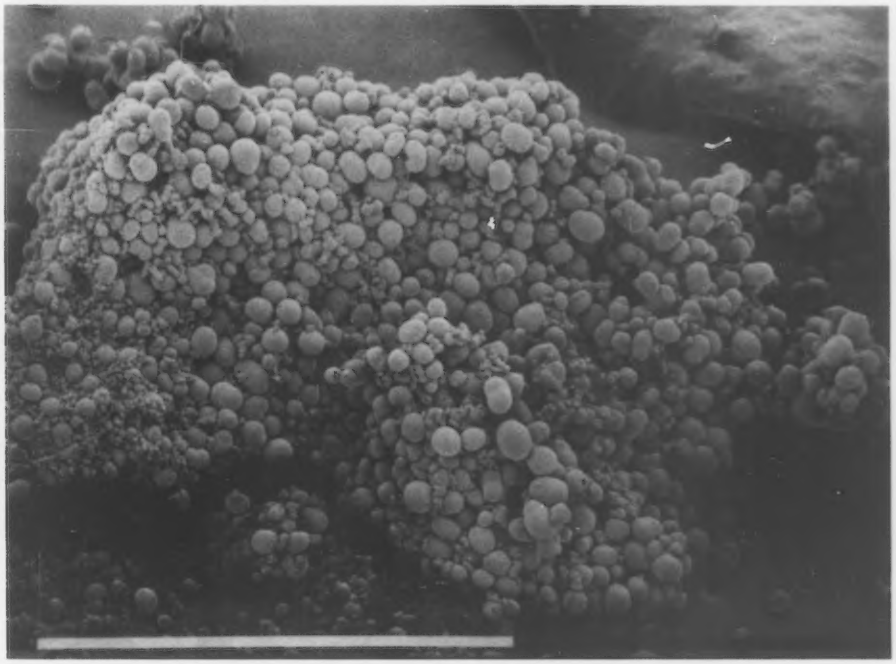


FIGURE 1B.—Broken portion of central mass of *Hydrolagus* otolith. Closed arrow indicates pockmarked features on the surface of the otoconium. The internal morphology of otolith consists of otoconia fused together (open arrow). Bar = 0.1 mm.

FIGURE 1C.—Mass of otoconia from *Harriotta*. Bar = 1 mm.



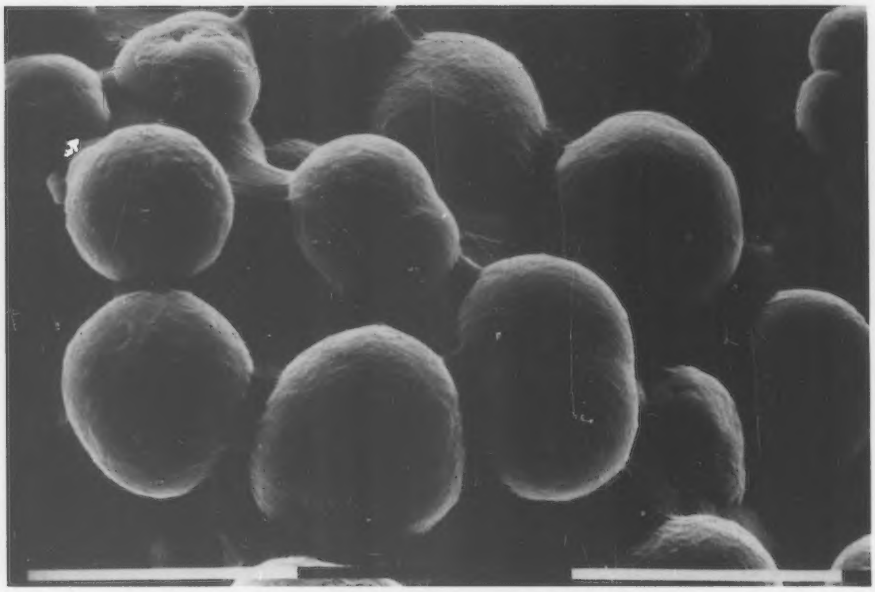


FIGURE 2A.—*Rhinochimaera* sp. otolith showing the encapsulation of otoconia by the matrix. Bar = 0.1 mm..

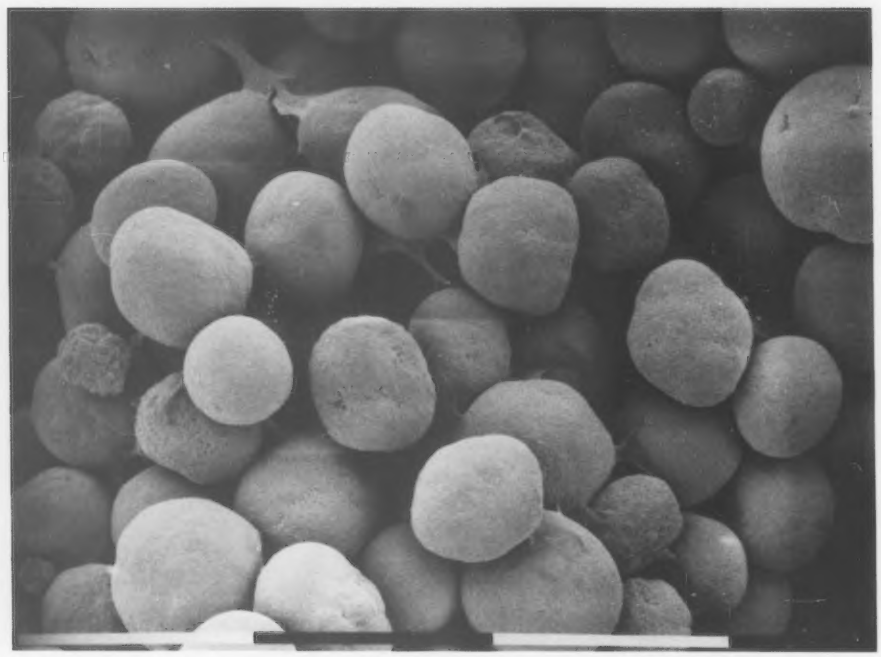


FIGURE 2B.—Otoconia of *Chimaera* sp. have little encapsulating matrix. Bar = 0.1 mm.

A dense aggregation of otoconia occurred within the otoliths of *Rhinochimaera* sp., each otoconia having a distinctive pockmarked surface topography (Fig. 3A). Surface otoconia (see Figure 2A) lacked these pockmarked features. At high magnifications, the pockmarked surface could be seen more clearly (Fig. 3B). In some cases the pockmarks resulted in enough material being removed from the surface to show that otoconia were deposited as layers (Fig. 3C). A few otoconia showed small ($\simeq$ 1 μm) spherules on their surface and some indications of fusion of the spherules into a distinct layer (Fig. 3B, D). Broken otoconia showed the expected epitaxial growth of crystals from a central point. The growth of individual otoconia appeared to be parallel to that of the otolith: small spherules ($\simeq$ 1 μm) continued to grow (1 μm) and progressively fuse into larger otoconia, which in turn fused to the form of the otolith itself (Fig. 3E).

The otoconia from *H. novaezelandiae* had a greater size range than those of *Rhinochimaera* sp. and *H. raleighana* and were more oval in shape. Although small ($\simeq$ 1 μm) spherules occurred on the surface of otoconia, they did not assume the more coordinated, layered appearance seen on the otoconia from *Rhinochimaera* sp. and may have represented recrystallization.

At similar magnifications to *Rhinochimaera* sp. and *H. novaezelandiae*, individual otoconia of *H. raleighana* showed a smooth and uniform surface. However, numbers of small crystals with variable shapes were commonly found in the otoconial mass of *H. raleighana*. Among these crystals were many rod-shaped and twinned rod-shaped crystals, some of which had small, surface recrystallizations on them (Fig. 4A). Crystalline aggregations occurred amongst the *H. raleighana* otoconia, which had the appearance of being part spindle-shaped aragonite crystal, part aragonite spherule, and part fused rod-shaped crystal (Fig. 4B).

The majority of otoconia observed from *Chimaera* sp. were regular spheres. On closer examination, the surfaces of *Chimaera* sp. otoconia varied from smooth to crystalline, and some otoconia surfaces exhibited a highly textured, irregularly crenellated surface (Fig. 5A). Deposits of irregularly formed otoconia occurred in *Chimaera* sp.; they were marked by the absence of any readily observable matrix binding and by the appearance of partially eroded

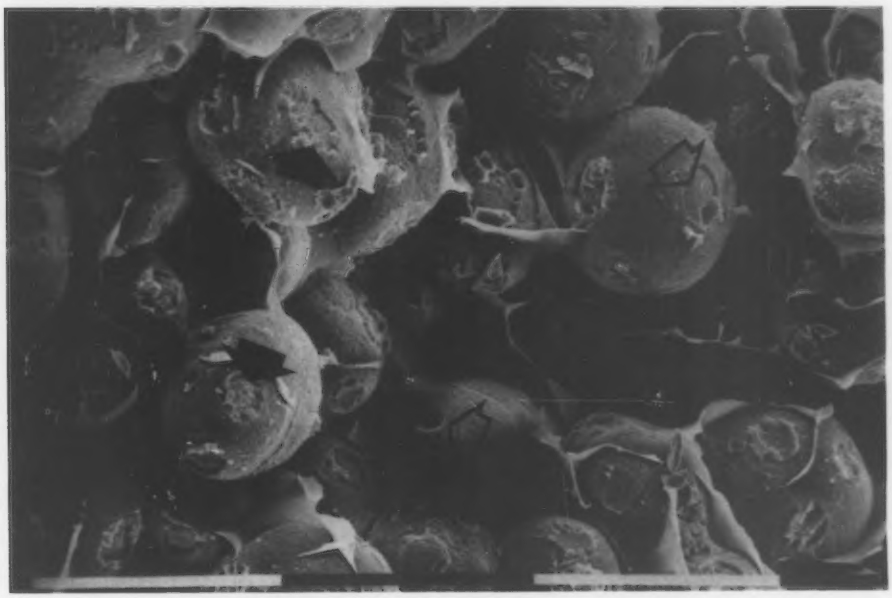


FIGURE 3A.—Otoconia from *Rhinochimaera* sp. have a distinctive pockmarked appearance, that shows possible points of adhesion (closed arrows) and other occurrences on the surface of the otoconia (open arrows) Bar = 0.1 mm.

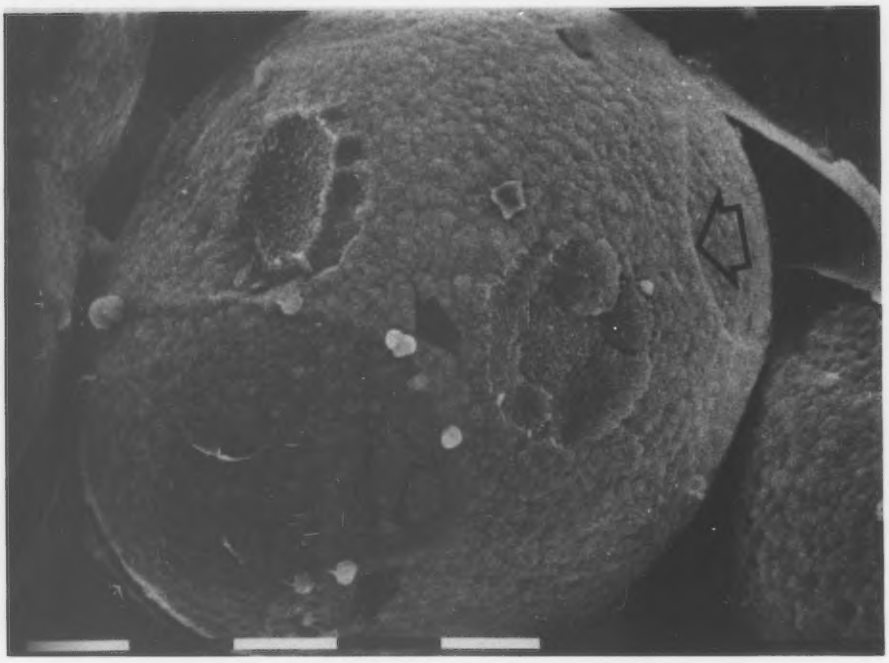


FIGURE 3B.—Small spherules (arrows) appear on the surface of the otoconia from *Rhinochimaera* sp. The body of the otoconia itself appears to be formed by the fusion of such small spherules, which may account for the smoothly bounded depressions (open arrows) on the surface as well as for the more obvious pockmarks. Bar = 10 μm.

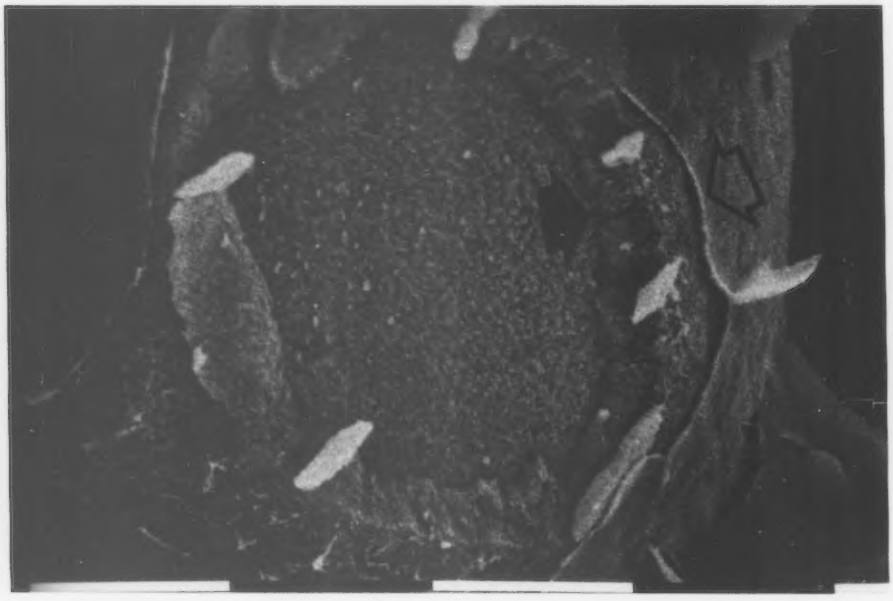


FIGURE 3C.—Small *Rhinochimaera* sp. otoconia show an apparently layered surface (closed arrow) and an enveloping matrix (open arrow). Bar = 10 μm.

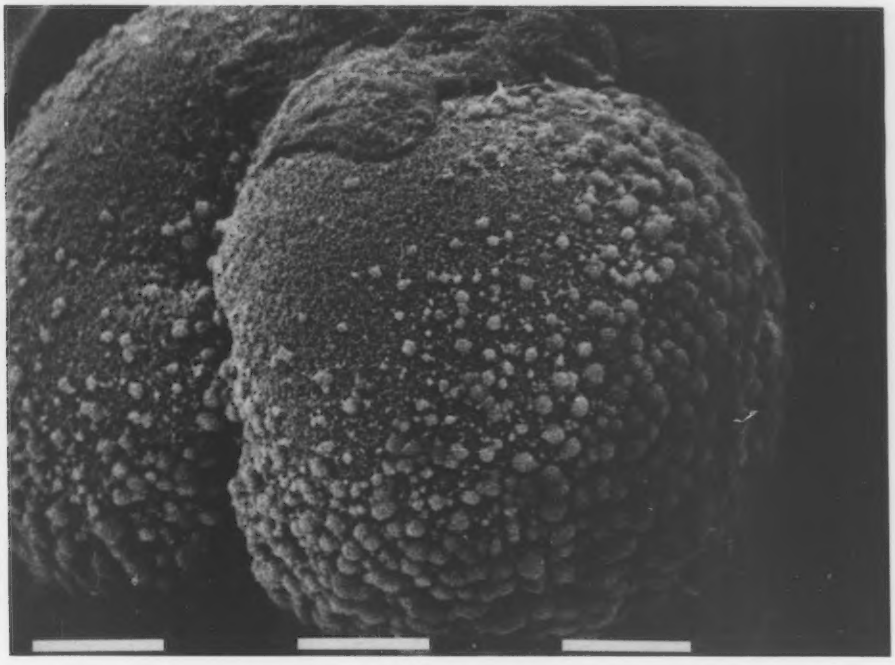


FIGURE 3D.—Some otoconia from *Rhinochimaera* sp. have surfaces formed of many small (≃ 1 μm) spherules which have yet to fuse to form the next smooth layer of surface. Bar = 10 μm.

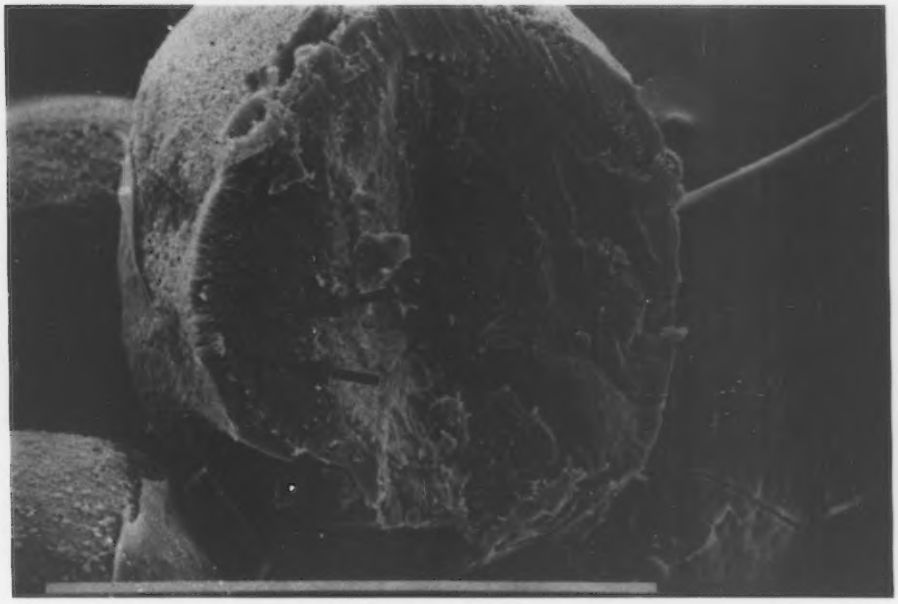


FIGURE 3E.—Broken otoconia from *Rhinochimaera* sp. show a radiating crystal structure with faint traces of small spherules (arrows). Bar = 0.1 mm.

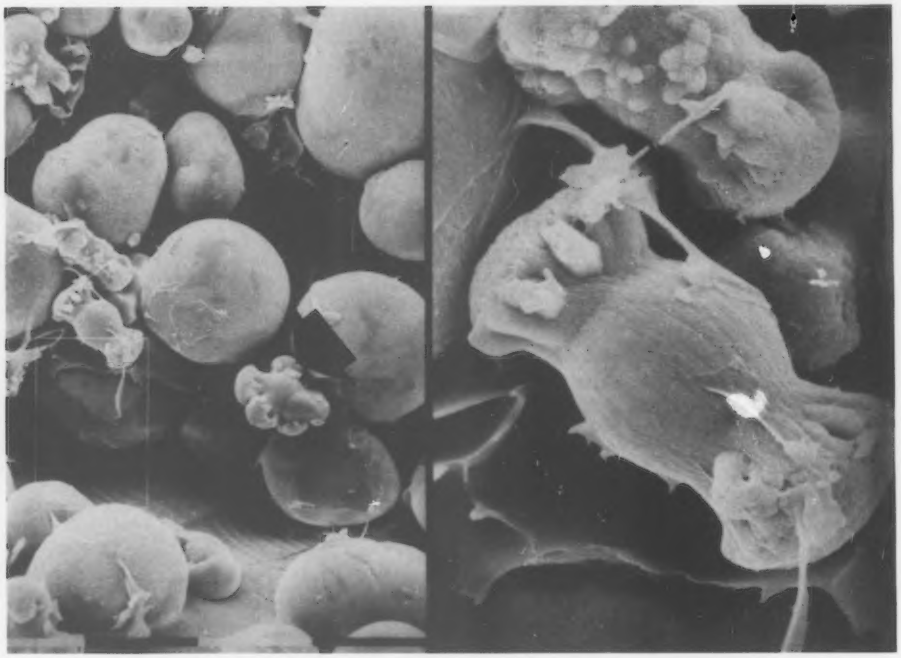


FIGURE 4A.—The round otoconia of *Harriotta raleighana* are very smooth compared with the otoconia of other chimaeras. An unusual rod-shaped crystal occurs in association with the otoconia which has a single (small closed arrow) and twinned (large closed arrow) form. In the higher magnification section the rod shaped crystals show further recrystallization on their surfaces. Bar = 10 μm.

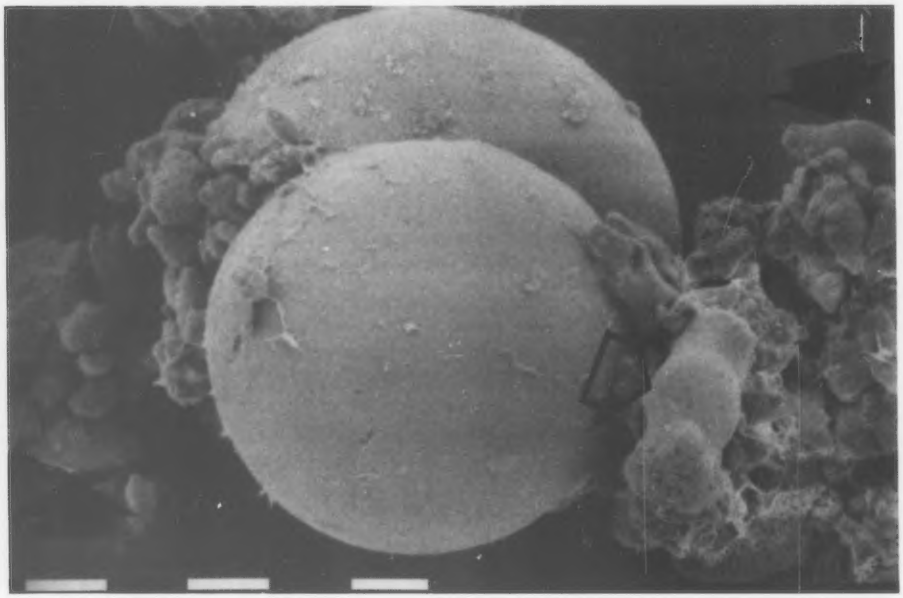


FIGURE 4B.—Crystalline aggregates of the rod-shaped crystal (open arrow) and apparent aragonite spindles (closed arrows) are found in association with the typical aragonite spherule type crystals. Bar = 50 μm.

spindle-shaped aragonite crystals (Fig. 5B). X-ray diffraction studies of the chimaeriform otoconia examined, including *Chimaera* sp., indicated that all of the calcium carbonate present was in the aragonite form.

Mean otoconial diameters of all four species of

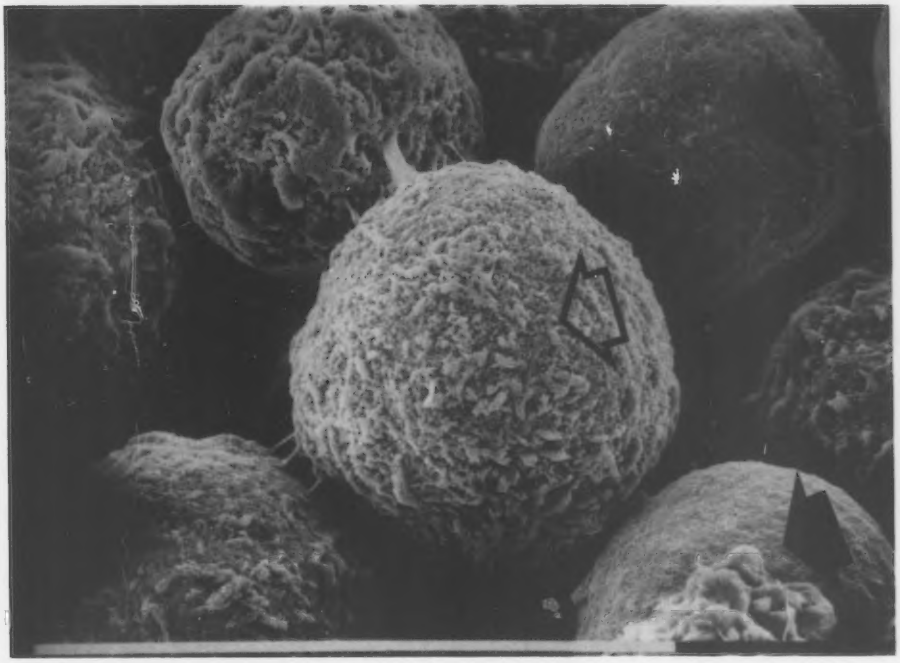


FIGURE 5A.—Otoconia from *Chimaera* sp. include both smooth (closed arrows) and highly textured (open arrow) otoconia. Bar = 0.1 mm.

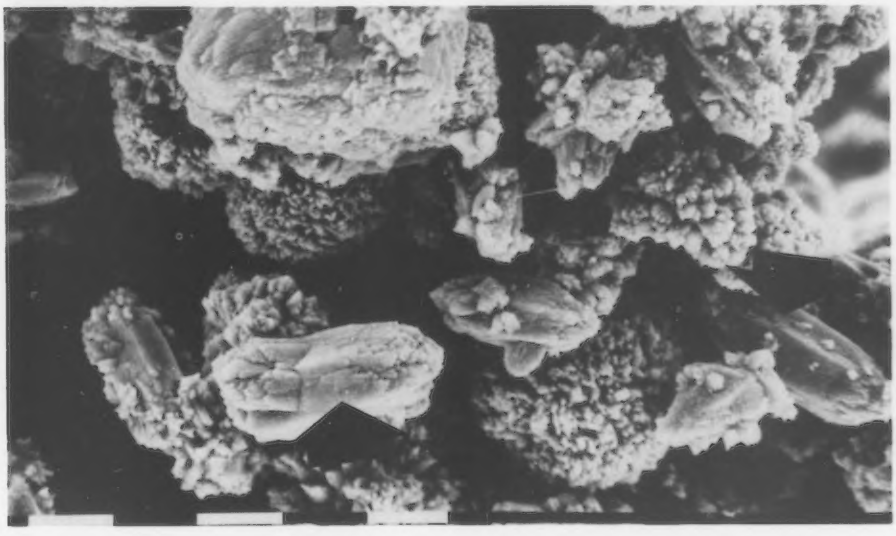


FIGURE 5B.—Parts of the otolith of *Chimaera* sp. are composed of small otoconia of the highly textured type as well as what appear to be partially eroded free aragonite crystals (arrows). Bar = 10 μm.

Chimaeriformes are listed in Table 1. A *t*-test weighted for unequal variances (Sokal and Rohlf 1969) shows statistically significant differences in the diameters of otoconia from different species ($P \leq 0.05$).

been described in the shark *Somniosus pacificus* (Lowenstam 1980), albeit with a distinctive polycrystalline appearance at the SEM level that is distinctively different from the aragonite spherule otoconia of chimaeras.

TABLE 1.—Mean otoconial diameters (μm) of all four species of Chimaeriform fish. n = sample size, $\bar{x}$ = mean otoconial diameter, SD = standard deviation.

Species	n	$\bar{x}$	SD	t	t(.05,49)
Rhinochimaera sp.	50	66.72	4.91		
				→3.6756	
Harriotta raleighana	50	62.19	7.20		2.0094
				→9.1056	
Chimaera sp.	50	50.26	5.83		
				→1.4738	
Hydrolagus novaezelandiae	50	48.19	8.04		

DISCUSSION

Carlström (1963) described the otoconia of *Chimaera monstrosa* as "almost perfect aragonite spheres". This study at the SEM level confirmed the generally spherical nature of chimaeriform otoconia that was observed at the light microscope level, and revealed considerable detail in variation in size, shape, and crystallinity of otoconia from four species of chimaeriforms.

There was a statistically significant variation in the diameters of otoconia amongst the species examined. In part, this variation reflected the relative amounts of small and large otoconia in the different species, as well as the maximum size of otoconia. Size variation in otoconia may represent physiological differences between individuals of the same species, interspecific differences, and perhaps age differences. Testing these alternatives was not possible with the samples at our disposal.

The predominant type of otoconia among the samples examined was more or less spherical, 40–70 μm in diameter. It was similar in size and in shape to otoconia described in the lungfish (Gauldie et al. 1986a), in the chimaera *C. milii* (Gauldie et al. 1987), and in a number of teleost species (Dale 1976; Gauldie et al. 1986b). X-ray diffraction studies showed that the spherule otoconia were formed from aragonite. Aragonitic spherule otoconia occurred in the chimaera *C. milii* (Gauldie et al. 1987) and in the lungfish *N. forsteri* (Gauldie et al. 1986a). However, spherule shaped otoconia composed of vaterite have

The rod-shaped crystals found in the otoconial mass of *H. raleighana* have not been described in the literature. It is possible that they were bacteria or some other organism. However, their crystalline appearance, which included twinning and surface recrystallization (Fig. 4B), as well as their apparent fusion with the spindle and spherule forms of aragonite, strongly suggest that they are some form of crystal.

There was considerable variation in the surface texture of the otoconia amongst the species described here and those described elsewhere. The otoconia of *H. raleighana* had the smoothest surface texture, but were among the larger otoconia. Therefore, one could reasonably conclude that variation in surface texture may not be due to the rate of crystal growth. In addition, otoliths of *Chimaera* sp. consisted of otoconia of about the same size, but with greatly differing surface texture. We have assumed that during storage the fluids of the endolymphatic sac were alkaline, but it is possible that in the stress of trawling the endolymph may have become acidic. Thus, variation in surface texture may be a preservation artifact. However, the similarity of the appearance of the surface texture of otoconia to those described from other studies, using different preservation techniques, suggests that erosion and recrystallization had not occurred. We conclude that the texture of the otoconia surface does not reveal any useful information about the growth rate of otoconia, but that it may provide clues to probable growth mechanisms.

For example, the layered appearance of some

otoconia may have been due to incremental growth. It was similar to the layered appearance of the lungfish otoconia (Gauldie et al. 1987) and to the layered appearance of statoconia in some mollusc species (Geuze 1968). If there was incremental growth of the otoconia, it indicates that, even at the most primitive level, the calcium metabolism of the inner ear has a definite periodicity. However, there is a major difference between the growth process of otoconia in the chimaera and that of statoconia in the mollusc (Kuzirian et al. 1981): the aragonitic otoconia of the chimaera obviously grows (and fuses into an otolith) in situ. The otoconia of the chimaera otolith often showed small surface crystals that apparently fuse together, implying continuous growth in situ, which is characteristic of teleost otoliths.

It can be assumed that a rigid otolith is required if the otolith functions as a sound transducer (Fay 1983) and that, in contrast, a loose aggregation of otoconia serves as a tilt, or angular momentum detection mechanism (Marmo 1983). The otoliths of the four species described here are rigid in comparison to those of *C. milii* (Gauldie et al. 1987), less rigid than the lungfish otoliths (Gauldie et al. 1986), and much more rigid than the loose and friable aggregations of otoconia that occur in most sharks and rays (Mulligan and Gauldie 1989). One might therefore conclude from our observations that the otoliths of chimaerids were functionally at a stage between a rigid sound transducer of the teleost type (which is found also in the lungfish) and an angular momentum detection mechanism.

The presence of spindle-shaped aragonite crystals in the otolith of *Chimaera* sp. is a particularly interesting observation because both spindle-shaped and spherule-shaped aragonite otoconia occur together with calcite crystals in the lungfish otolith. "Aragonite spherule" otoconia have also been described for the primitive shark *Heptanchus cinereus* (Nishio 1926) and have been observed (Mulligan and Gauldie 1989) in the related *Heptranchias perlo* of New Zealand waters. Furthermore, aggregated spherulitic otoconia have been observed in humans with congenital hearing disorders (Johnsson et al. 1981) and are difficult to distinguish visually from otoconial aggregations in chimaeras and some teleosts (Gauldie et al. 1986b).

It is tempting to see parallels between the otoconia of chimaeras, lungfish, and primitive sharks. However, the nature of evolutionary processes (particularly convergence processes) does not allow simple extrapolation of "primitive" features, and hence phylogenetic reconstruction, from modern species (Cain 1983). This is particularly true when the physiological effects of otoconia types on inner ear function are completely unknown. However, it is clear that the spherulitic otoconia and otic organization of chimaeriform fish have chemical and anatomical parallels with the inner ear of teleost fish in the orders Cheilodactylidae, Moridae, Gadidae, Balistidae, and Gempylidae; with some sharks; and, rarely, with humans. The occurrence of spindle shaped aragonite otoconia in conjunction with spherule otoconia has a parallel in the otoconia of the lungfish. Such similarities makes it very difficult to assign any taxonomic value to otoconia types. Perhaps spherulitic otoconia represent one of very few successful calcium carbonate matrix/mineralization systems which converge in so many vertebrates simply because there are so few alternatives.

ACKNOWLEDGMENTS

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Feeding Habits of Whitebone Porgy, *Calamus leucosteus* (Teleostei: Sparidae), Associated with Hard Bottom Reefs off the Southeastern United States[1]

George R. Sedberry

ABSTRACT: The feeding habits of whitebone porgy, *Calamus leucosteus*, were investigated by examining stomachs of specimens collected from hard bottom reef habitat on the southeastern continental shelf and by comparing stomach samples with benthic samples and with stomach samples from four other sparids collected from the same habitat. Whitebone porgy were found to feed mainly on small hard-shelled species of gastropods, pagurid decapods, and sipunculids. Polychaetes, pelecypods, barnacles, and fishes were also eaten. Fishes and echinoderms were consumed by larger individuals. Whitebone porgy selected invertebrate species that were not abundant in benthic samples from the reef, suggesting that these fish forage on sand bottom fauna. Patterns of diet overlap with other reef-associated sparids appeared to be related to feeding morphology and feeding habitat. Overlap in diet between whitebone porgy and southern porgy, *Stenotomus aculeatus*, was low, although both species forage on sand bottom organisms. Pinfish, *Lagodon rhomboides*, fed mainly on a sessile reef amphipod that was rarely consumed by whitebone porgy. Whitebone porgy had a higher diet overlap with sheepshead, *Archosargus probatocephalus*, and with red porgy, *Pagrus pagrus*, because all three species fed on barnacles not consumed by other sparids examined.

The whitebone porgy, *Calamus leucosteus*, distributed from the Carolinas through the Gulf of Mexico (Randall 1978), is an abundant sparid fish on the continental shelf of the South Atlantic Bight, where it is an important component of trawl and hook-and-line fisheries (Huntsman 1976; Waltz et al. 1982). Whitebone porgy are found in depths of 11–88 m on the continental shelf of the southeastern coast of the United States, but they are most abundant in depths < 30 m (Waltz et al. 1982). The continental shelf at these depths consists primarily of sandy bottom, with occasional scattered outcrops of sedimentary rock (Struhsaker 1969), and, although whitebone porgy frequently occur on sand bottom, they are much more abundant in rocky reef habitats (Wenner et al. 1980; Waltz et al. 1982). These hard bottom habitats support a greater abundance and biomass of large sessile invertebrates (e.g., sponges, corals, tunicates) and associated motile organisms than do sand bottom areas of the shelf (Struhsaker 1969; Wenner 1983; Wenner et al. 1983; Sedberry and Van Dolah 1984; Wenner et al. 1984; Wendt et al. 1985). Many of these invertebrates serve as prey for fishes that are closely associated with the reef habitat (Manooch 1977; Sedberry 1987, 1988). Other species of fishes are less closely associated with hard bottom reefs, and, while living on or in proximity to these reefs, do much of their foraging in sand bottom habitats on the shelf (Sedberry 1985). Although whitebone porgy appear to be a reef-associated species, their dependence on reef habitat and the abundance of prey provided by these habitats are unknown. Although hard bottom reefs support a high biomass of potential prey for fishes, many species of predatory fish are concentrated in these habitats (Sedberry and Van Dolah 1984), and competition for prey may be intense, particularly among closely related species. Several other sparids are abundant in hard bottom reef communities and competition for food among these species could be as intense. Although the food habits of some of these more common sparids have been reported from offshore reef habitats (Manooch 1977; Sedberry 1987), overlap in diet among the species has not been investigated.

The purpose of this study is to describe the food habits of whitebone porgy, to determine the importance of hard bottom reef habitat as foraging grounds for this species, and to determine diet overlap between whitebone porgy and some

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other abundant sparid fishes from the same habitat.

METHODS

Stomachs of fish analyzed for food habits were collected during six trawl cruises on the continental shelf in 1980 and 1981. Stomachs of whitebone porgy were taken at 11 hard bottom stations distributed among 3 depth zones representing the inner shelf (16–22 m depth, three stations), middle shelf (23–37 m depth, four stations), and the outer shelf (46–69 m depth, four stations). Delineation of depth zones was based on distribution of fish and invertebrate species assemblages as noted in previous studies and on community analysis of trawl catches used in the present study (Struhsaker 1969; Miller and Richards 1980; Sedberry and Van Dolah 1984; Wenner et al. 1984). Fishes were collected primarily in trawl tows as described elsewhere (Sedberry and Van Dolah 1984; Wenner et al. 1984; Sedberry 1985). A few specimens were collected with trap or hook and line. Sampling for fishes was conducted on hard bottom habitat, which was mapped for each station using underwater television (Sedberry and Van Dolah 1984).

Whitebone porgy were measured (standard length, SL) at sea, and their stomachs were preserved in 10% seawater formalin. Contents of individual stomachs were then sorted in the laboratory by taxa, counted, and measured volumetrically. The relative contribution of food items to the diet was described by percent frequency occurrence (F), percent numerical abundance (N), and percent volume displacement (V). F, N, and V were calculated for prey species and for prey items grouped into higher taxonomic categories, for 50 mm intervals of SL.

In order to determine the selectivity or dependence of demersal fishes on hard bottom prey organisms, stomach samples were compared with benthic samples using Ivlev's index of electivity (Ivlev 1961). Electivity values range from −1 to +1. Negative values imply that the prey species is avoided by the predator or that it is unavailable to the predator. Positive values imply that the predator prefers the prey species or that it is feeding on prey species that occur in a different habitat than that sampled by the benthic sampler. A value near zero implies no selectivity by the predator; i.e., the fish is feeding on the prey in proportion to the prey's relative abundance in samples taken in the habitat.

The electivity index was calculated for species that were numerically dominant in benthic samples or in fish stomach samples which were pooled by depth zone (inner, middle, and outer shelves) for comparison. Benthic samples were obtained at the 11 hard bottom sites during 1980 and 1981 with a suction device (inner and middle shelves) or a grab (outer shelf). Divers obtained five replicate suction samples at each inner and middle shelf station by scraping the hard substrata enclosed by a 0.1 m^2 quadrat box, while simultaneously sucking with an airlift device similar to that described by Chess (1979). Suction samples were collected in 1.0 mm mesh bags. At the outer shelf stations where water depth precluded the use of the suction device operated by divers, quantitative samples (five copies) were collected with a 0.1 m^2 Smith-McIntyre grab. After retrieval, each sample was placed into a 1.0 mm sieve and washed to remove the finer sediment.

Sampling motile benthic invertebrates with the suction sampler proved to be a very simple, yet effective, technique. Samples were quantitative because suctioning effectively collected everything within the confines of the walled box placed on the substratum. The Smith-McIntyre grab, which was substituted for the suction sampler at deeper stations, was somewhat less quantitative because the sampler is not as effective on hard substrate, and the actual area sampled was unknown. In spite of these limitations, the grab sampler was the only feasible means of sampling the benthos at outer shelf stations and provided the only benthic collections with which to calculate electivity.

Similarity in diet between whitebone porgy and four other co-occurring and frequently collected sparids was also investigated. Stomach samples of these additional species were collected at the same time as the whitebone porgy stomachs and were analyzed in a similar manner (South Carolina Wildlife and Marine Resources Department 1984; Sedberry 1987). These other sparids were sheepshead, *Archosargus probatocephalus;* pinfish, *Lagodon rhomboides;* red porgy, *Pagrus pagrus*; and southern porgy, *Stenotomus aculeatus.*

Similarity in diet between these sparids was measured using the Bray-Curtis measure (Bray and Curtis 1957). Because sample sizes of predators were unequal, abundance of prey items was standardized as percent numerical abundance for each predator, resulting in values of percent similarity in composition of diet between pairs of

predator species (Clifford and Stephenson 1975; Boesch 1977). Only prey items that were identified to species were included in the similarity analyses. To reduce the data matrix to a size that could be accommodated by the computer program and to eliminate very rare prey species that were not important in the diet of any sparid, only prey species that occurred more than once were included in the analysis.

RESULTS

Whitebone porgy were common in all three depth zones, but they were more abundant at middle and outer shelf stations (5.6 and 5.8 fish per tow, respectively) than on the inner shelf (2.6 fish per tow). Other sparids examined overlapped in depth distribution with whitebone porgy. Sheepshead occurred at inner (1.7 fish per tow) and middle (0.2 per tow) shelf stations. Pinfish (6.2, 1.1, and < 0.1 fish per tow for inner, middle, and outer shelf stations, respectively) and southern porgy (376.8, 562.8, and 0.9 fish per tow) occurred in all three depth zones; red porgy was collected only on the middle (1.4 fish per tow) and outer (5.6 fish per tow) shelf stations.

Whitebone porgy stomachs (N = 219) contained at least 135 species of invertebrates and fishes. Decapods were the most important prey and ranked high in frequency, number, and volume (Table 1). Very small hermit crabs (*Pagurus* spp., *Dardanus* spp., *Paguristes* spp., *Pylopagurus* spp., other Paguroidea) were the dominant decapods in whitebone porgy stomachs, and they sometimes were found along with their gastropod shells, which were usually very damaged. Gastropods were important prey and sipunculids, especially the species *Aspidosiphon gosnoldi* which occupies gastropod shells, were frequently consumed. Gastropods and *Aspidosiphon* sipunculids were often found without their shells. Because mollusk shells were infrequently swallowed by whitebone porgy, many gastropods and pelecypods could not be identified. The gastropod *Costoanachis avara* was the most abundant identifiable mollusk in whitebone porgy stomachs. Other important prey for whitebone porgy included polychaetes, pelecypods, barnacles, and fishes.

TABLE 1.—Percentage of frequency occurrence (F), percentage of number (N), and percentage of volume (V) of prey items and higher taxonomic groups of food in the diet of whitebone porgy, *Calamus leucosteus*.

Taxon Prey item	F	N	V
Algae undetermined	1.3	0.2	<0.1
Porifera undetermined	0.6	0.1	0.2
Cnidaria			
Hydrozoa			
Dynamena sp.	0.6	0.1	<0.1
Halecium sp.	1.3	0.2	<0.1
Total Hydrozoa	1.9	0.2	<0.1
Anthozoa			
Actiniaria undetermined	5.7	0.7	1.5
Athenaria undetermined	8.2	2.4	4.5
Renilla reniformis	1.3	0.2	2.6
Total Anthozoa	15.1	3.3	8.6
Nemertinea undetermined	1.3	0.4	2.0
Annelida			
Polychaeta			
Aglaophamus verrilli	0.6	0.1	<0.1
Ampharete acutifrons	1.3	0.2	<0.1
Amphinomidae undetermined	0.6	0.1	<0.1
Arabella iricolor	0.6	0.1	0.2
Arabella mutans	1.9	0.2	1.0
Arabellidae undetermined	0.6	0.1	0.2
Armandia maculata	0.6	0.2	<0.1
Capitellidae undetermined	0.6	0.1	0.1
Cirratulidae undetermined	1.9	0.2	0.3

Taxon Prey item	F	N	V
Polychaeta—*Con.*			
Diopatra cuprea	1.9	0.2	0.5
Dodecaceria corallii	0.6	0.1	<0.1
Eunice vittata	1.3	0.2	<0.1
Eunicidae undetermined	0.6	0.1	<0.1
Glycera americana	0.6	0.1	<0.1
Glycera sp.	0.6	0.2	0.1
Hydroides crucigera	0.6	0.1	<0.1
Leiochrides pallidior	0.6	0.2	<0.1
Lumbrineris coccinea	0.6	0.1	0.2
Lumbrineris inflata	0.6	0.1	<0.1
Lumbrineris latreilli	0.6	0.1	<0.1
Maldanidae undetermined	5.0	0.7	0.5
Nephtyidae undetermined	2.5	0.3	<0.1
Nephtys incisa	0.6	0.1	<0.1
Nereidae undetermined	0.6	0.1	<0.1
Nichomachinae undetermined	0.6	0.1	0.2
Onuphidae undetermined	1.3	0.2	1.5
Onuphis eremita	2.5	0.4	0.6
Onuphis nebulosa	1.3	0.6	0.4
Onuphis pallidula	0.6	0.1	<0.1
Onuphis sp.	1.3	0.2	<0.1
Opheliidae undetermined	0.6	0.1	<0.1
Paranaitis polynoides	0.6	0.1	<0.1
Petaloproctus socialis	0.6	0.1	<0.1
Phyllodoce longipes	0.6	0.1	<0.1

TABLE 1.—*Continued.*

Taxon Prey item	*F*	*N*	*V*
Annelida—*Con.*			
Polychaeta—*Con.*			
Phyllococe sp.	0.6	0.1	<0.1
Phyllodocidae undetermined	1.3	0.2	<0.1
Polychaeta undetermined	22.6	3.1	1.4
Polydora commensalis	0.6	0.1	<0.1
Psammolyce ctenidophora	0.6	0.1	0.3
Scalibregmidae undetermined	1.3	0.2	0.1
Sigalionidae undetermined	1.3	0.2	<0.1
Spionidae undetermined	0.6	0.1	<0.1
Sthenelais boa	0.6	0.1	<0.1
Sthenelais sp.	1.3	0.2	0.1
Syllidae undetermined	1.3	0.2	0.1
Syllis sp. F	0.6	0.1	<0.1
Terebellidae undetermined	0.6	0.1	0.4
Travisia parva	0.6	0.1	<0.1
Websterinereis sp.	1.3	0.2	<0.1
Total Polychaeta	46.5	9.6	8.6
Mollusca			
Gastropoda			
Buccinidae undetermined	1.3	0.2	0.1
Caecum pulchellum	0.6	0.1	<0.1
Calliostoma baridi	1.9	0.4	0.2
Cerithidea sp.	0.6	0.1	<0.1
Cymatium krebsii	0.6	0.2	<0.1
Costoanachis avara	6.9	2.1	0.2
Costoanachis sp.	0.6	0.1	<0.1
Diodora cayenensis	0.6	0.1	0.5
Epitonium sp.	3.1	2.0	0.4
Epitonium multistriatum	0.6	0.1	<0.1
Fissurellidae undetermined	0.6	0.1	0.2
Gastropoda undetermined	46.5	13.8	7.7
Marginella sp.	1.3	0.2	0.1
Marginella hartleyanum	3.8	1.8	0.9
Marginellidae undetermined	1.9	0.3	0.2
Natica canrena	1.9	0.4	0.2
Naticidae undetermined	4.4	1.1	0.8
Trochidae undetermined	0.6	0.1	<0.1
Total Gastropoda	58.5	23.0	11.4
Pelecypoda			
Americardia media	0.6	0.1	<0.1
Anadara sp.	0.6	0.1	0.7
Brachidontes sp.	0.6	0.1	<0.1
Chione latilirata	1.3	0.2	<0.1
Corbula contracta	3.1	0.5	0.3
Corbula dietziana	0.6	0.2	0.2
Dinocardium robustum	1.9	0.2	0.3
Ervilia concentrica	2.5	0.4	0.3
Glycymeris pectinata	0.6	0.1	<0.1
Laevicardium sp.	0.6	0.2	0.2
Laevicardium laevigatum	3.1	0.5	0.4
Laevicardium pictum	2.5	0.4	0.4
Pectinidae undetermined	1.9	0.2	0.2
Pelecypoda undetermined	11.3	2.0	4.9
Pitar fulminatus	0.6	0.1	<0.1
Pleuromeris tridentata	0.6	0.1	<0.1
Solemya velum	0.6	0.1	0.2
Solenidae undetermined	0.6	0.1	<0.1
Tellina sp.	1.9	0.3	0.1
Total Pelecypoda	21.4	5.6	8.4
Cephalopoda undetermined	0.6	0.1	<0.1
Crustacea			
Ostracoda undetermined	0.6	0.2	<0.1
Copepoda undetermined	0.6	0.1	<0.1
Cirripedia			
Balanoidea undetermined	1.3	0.4	0.5
Balanus sp.	1.9	0.2	<0.1
Balanus trigonus	10.7	5.0	2.6
Balanus venustus	6.3	3.4	1.8
Total Cirripedia	14.5	9.0	5.0
Stomatopoda undetermined	2.5	0.4	0.2
Mysidacea			
Bowmaniella portoricensis	1.9	0.4	<0.1
Mysidae undetermined	0.6	0.1	<0.1
Total Mysidacea	2.5	0.4	<0.1
Cumacea			
Bodotriidae undetermined	0.6	0.1	<0.1
Cyclaspis varians	0.6	0.1	<0.1
Oxyurostylis smithi	4.4	0.7	<0.1
Total Cumacea	5.7	0.8	<0.1
Isopoda			
Apanthura magnifica	0.6	0.1	<0.1
Total Isopoda	0.6	0.1	<0.1
Amphipoda			
Ampelisca sp.	2.5	0.3	<0.1
Ampelisca cristoides	1.3	0.2	<0.1
Ampelisca schellenbergi	0.6	0.1	<0.1
Ampelisca vadorum	1.9	0.3	0.1
Ampelisca venetiensis	0.6	0.2	0.1
Carinobatea carinata	0.6	0.1	<0.1
Caprellidae undetermined	0.6	0.1	<0.1
Corophiidae undetermined	0.6	0.2	<0.1
Elasmopus sp. A	0.6	0.1	<0.1
Erichthonius sp. A	1.3	0.2	<0.1
Erichthonius brasiliensis	2.5	0.3	<0.1
Gammaridea undetermined	3.8	0.6	<0.1
Haustoriidae undetermined	1.9	0.2	<0.1
Lembos smithi	0.6	0.1	<0.1
Lembos spinicarpus inermis	0.6	0.1	<0.1
Lembos unicornis	0.6	0.1	<0.1
Melita appendiculata	0.6	0.1	<0.1
Metharpinia floridanus	1.9	0.4	0.1
Photis sp.	0.6	0.1	<0.1
Phtisica marina	1.9	0.2	<0.1
Podocerus sp. A	0.6	0.1	<0.1
Rhepoxynius epistomus	0.6	0.1	<0.1
Tiron tropakis	0.6	0.1	<0.1
Total Amphipoda	21.4	3.8	0.4

TABLE 1.—*CONTINUED.*

Taxon Prey item	*F*	*N*	*V*
Crustacea—*Con.*			
Decapoda			
Albunea sp	1.3	0.2	0.4
Alpheidae undetermined	1.3	0.3	0.2
Anomura undetermined	0.6	0.2	<0.1
Automate sp.	0.6	0.1	<0.1
Brachyura undetermined	17.0	2.3	3.0
Calappidae undetermined	0.6	0.1	0.1
Callianassa sp.	0.6	0.1	<0.1
Callianassa atlantica	1.3	0.2	0.4
Caridea undetermined	0.6	0.1	<0.1
Dardanus sp.	1.9	0.4	0.1
Diogenidae undetermined	0.6	0.1	<0.1
Dissodactylus mellitae	0.6	0.1	<0.1
Euceramus praelongus	0.6	0.1	0.1
Hepatus epheliticus	1.3	0.2	0.8
Hippidae undetermined	0.6	0.1	<0.1
Hypoconcha arcuata	3.1	0.5	1.3
Iridopagurus dispar	3.1	1.1	0.3
Leptochela sp.	1.9	0.2	<0.1
Leptochela papulata	3.1	1.1	0.4
Majidae undetermined	2.5	0.3	0.4
Mithrax pleuracanthus	0.6	0.1	0.7
Munida irrasa	0.6	0.1	<0.1
Natantia undetermined	5.7	0.7	0.6
Natantia undetermined zoea	0.6	0.1	<0.1
Osachila sp.	0.6	0.2	2.8
Osachila tuberosa	0.6	0.4	0.2
Paguridae undetermined	13.2	2.8	0.7
Paguridea undetermined	8.8	1.2	0.2
Paguristes sp.	1.3	0.2	0.1
Paguristes tortugae	1.3	0.2	<0.1
Pagurus sp.	12.6	3.4	0.8
Pagurus carolinensis	17.0	3.3	0.7
Pagurus hendersoni	17.0	5.1	0.9
Pagurus longicarpus	0.6	0.1	<0.1
Pagurus piercei	2.5	0.3	0.2
Panulirus sp. larvae	0.6	0.1	<0.1
Parthenope sp.	0.6	0.1	0.3
Parthenopidae undetermined	1.3	0.2	0.1
Penaeidae undetermined	0.6	0.2	0.5
Periclimenaeus sp.	0.6	0.1	<0.1
Pilumnus dasypodus	0.6	0.1	<0.1
Pinnixa sp.	0.6	0.1	<0.1
Pinnotheres sp.	0.6	0.1	<0.1
Podochela gracilipes	0.6	0.1	0.1
Portunidae undetermined	2.5	0.3	0.5
Portunus spinicarpus	0.6	0.1	0.1
Pseudomedaeus agassizii	0.6	0.1	0.1
Pylopagurus sp.	0.6	0.1	<0.1
Pylopagurus corallinus	0.6	0.1	<0.1
Pylopagurus discoidalis	0.6	0.1	<0.1
Pylopagurus holthuisi	1.9	0.4	0.1
Synalpheus townsendi	0.6	0.1	0.1
Xanthidae undetermined	1.9	0.2	0.1
Total Decapoda	70.4	27.8	17.3
Crustacea undetermined	1.9	0.2	<0.1
Sipunculida			
Aspidosiphon gosnoldi	17.6	6.2	0.6
Phascolopsis gouldi	1.3	0.2	0.9
Sipunculida undetermined	3.1	0.4	1.5
Sipunculus nudus	0.6	0.1	2.7
Total Sipunculida	22.6	7.0	5.8
Brachiopoda			
Glottidia pyramidata	2.5	0.6	0.1
Total Brachiopoda	2.5	0.6	0.1
Bryozoa			
Antropora tincta	0.6	0.1	<0.1
Bryozoa undetermined	0.6	0.1	<0.1
Diaperoecia floridana	0.6	0.1	<0.1
Hippoporidra janthina	2.5	0.3	0.1
Schizoporella cornuta	3.8	0.4	0.1
Total Bryozoa	6.3	1.0	0.2
Echinodermata			
Asteroidea			
Asteroidea undetermined	0.6	0.1	0.1
Astropecten sp.	3.8	0.4	3.2
Astropecten articulatus	1.9	0.2	1.4
Astropecten duplicatus	1.3	0.3	0.7
Echinaster sp.	1.9	0.3	0.5
Luidia sp.	0.6	0.1	0.5
Luidia alternata	1.9	0.2	2.1
Total Asteroidea	12.0	1.6	8.4
Echinoidea			
Clypeasteroida undetermined	0.6	0.1	<0.1
Echinoidea undetermined	3.1	0.4	1.7
Total Echinoidea	3.8	0.4	1.8
Ophiuroidea undetermined	17.6	2.0	1.2
Holothuroidea			
Holothuroidea undetermined	1.9	0.2	1.4
Thyone sp.	1.3	0.2	4.4
Total Holothuroidea	2.5	0.4	5.8
Chordata			
Ascidiacea undetermined	0.6	0.1	1.8
Pisces			
Bothidae undetermined	0.6	0.1	0.8
Decapterus punctatus	0.6	0.1	0.6
Ogcocephalus parvus	0.6	0.1	1.2
Synodus sp.	0.6	0.1	3.6
Teleostei undetermined	9.4	1.4	6.6
Fish scales	0.6	0.1	<0.1
Total Pisces	12.0	1.8	12.8
Number of stomachs examined		219	
Examined stomachs with food		159	

Whitebone porgy (99–315 mm SL) demonstrated slight changes in feeding habits with increasing size (Table 2). Anthozoans and barnacles (Cirripedia) appeared to be more frequent in the smallest size class, but this may be a result of the small sample of fish < 151 mm SL. Decapods were frequently consumed by all size classes; however, because most decapods eaten were tiny species of hermit crabs, this taxon contributed a much smaller proportion of the prey volume for fish larger than 150 mm SL. Gastropods and sipunculids were also consumed by all size classes. Fishes increased in volumetric importance in the diet of fish up to a length of 250 mm but were not frequently consumed by the largest fish. Echinoderms were more important in the diet of larger whitebone porgy.

Suction and grab samples from the hard bottom stations were dominated by tube-reef building polychaetes, such as *Filograna implexa*, *Phyllochaetopterus socialis*, and *Pista palmata*, as well as epifaunal amphipods (*Erichthonius brasiliensis*, *Luconacia incerta*) that cling to or build tubes on hard substrates or other epibenthic organisms. These species were generally not consumed by whitebone porgy in any

TABLE 2.—Percentage of frequency occurrence (*F*), percentage of number (*N*), and percentage of volume (*V*) of higher taxonomic groups of food in the diet of whitebone porgy, by length interval.

	Length intervals (mm SL)											
	<151			151–200			201–250			>250		
Prey	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*
Algae							3.2	0.3	<0.1			
Porifera										2.3	0.3	0.3
Cnidaria												
Hydrozoa				4.4	0.6	<0.1				2.3	0.3	<0.1
Anthozoa	37.5	9.8	10.0	10.9	4.4	14.8	14.5	2.4	5.8	16.3	2.9	9.2
Nemertinea				2.2	1.1	12.7	1.6	0.2	0.3			
Annelida												
Polychaeta	25.0	9.8	6.9	47.8	9.4	11.6	48.4	8.8	6.8	46.5	11.1	9.3
Mollusca												
Gastropoda	12.5	2.4	0.2	58.7	26.9	16.2	66.1	24.9	11.2	55.8	17.9	10.4
Pelecypoda	12.5	9.8	14.4	21.7	4.2	12.0	22.6	5.8	7.6	20.9	6.4	7.8
Cephalopoda				2.2	0.3	0.1						
Crustacea												
Ostracoda										2.3	0.6	<0.1
Copepoda							1.6	0.2	<0.1			
Cirripedia	37.5	17.1	17.2	8.7	2.5	2.5	14.5	10.4	5.0	16.3	12.3	5.3
Stomatopoda	12.5	2.4	1.0				1.6	0.2	0.2	4.6	0.9	0.2
Mysidacea				8.7	1.7	0.2						
Cumacea				8.7	1.1	0.1	3.2	0.6	<0.1	7.0	0.9	<0.1
Isopoda							1.6	0.2	<0.1			
Amphipoda				17.4	4.2	0.8	29.0	4.3	0.5	18.6	2.9	0.2
Decapoda	50.0	26.8	43.3	71.7	31.7	14.2	71.0	23.0	11.4	72.1	32.8	22.8
Crustacea undetermined				6.5	0.8	0.1						
Sipunculida	12.5	17.1	6.9	23.9	6.7	4.2	33.9	9.5	11.4	7.0	1.5	1.2
Brachiopoda				2.2	0.8	0.2	3.2	0.6	0.1	2.3	0.3	<0.1
Bryozoa							14.5	1.8	0.4	2.3	0.6	0.2
Echinodermata												
Asteroidea				4.4	0.6	5.7	12.9	1.6	7.6	20.9	2.9	10.4
Echinoidea							4.8	0.5	0.4	7.0	0.9	3.6
Ophiuroidea	12.5	2.4	<0.1	15.2	1.9	0.8	21.0	2.1	2.4	16.3	2.0	0.4
Holothuroidea										9.3	1.5	13.1
Chordata												
Ascidiacea										2.3	0.3	4.0
Pisces	12.5	2.4	0.1	8.7	1.1	4.0	19.4	2.7	28.9	4.6	0.6	1.5
Number of stomachs examined		11			62			86			60	
Examined stomachs with food		8			46			62			43	
Mean length of fish with food		125.2			183.7			223.5			272.2	

of the three depth zones (Table 3). Rather, whitebone porgy fed selectively on hard-shelled invertebrate species that were collected only occasionally, or not at all, in suction and grab samples. Many of these prey species are apparently more common in sand bottom habitat (see Discussion).

Whitebone porgy displayed a relatively high similarity in diet to red porgy and sheepshead; overlap in diet with pinfish and southern porgy was low (Table 4).

DISCUSSION

Published information on the diet of *Calamus leucosteus* is lacking. Randall (1967) and Darcy (1986) reported on the food habits of several other Atlantic species of *Calamus* and noted a high incidence of shelled invertebrates such as mollusks, crabs, and echinoids in their diets. Randall (1967) also noted that those *Calamus* spp. which fed on hermit crabs were largely gastropod feeders as well and that sipunculids

TABLE 3.—Relative abundance (percentage of total number of individuals) and electivity values (E) for dominant benthic species in suction and grab samples and in whitebone porgy stomachs. Dominant species include those that ranked in the five most abundant species within stomach or benthic samples in any depth zone for collections pooled for all seasons and years.

	Inner shelf			Middle shelf			Outer shelf		
	Fish stomachs	Benthic samples	E	Fish stomachs	Benthic samples	E	Fish stomachs	Benthic samples	E
Dominant species—benthic samples									
Chone americana	—	0.33	−1.00	—	0.81	−1.00	—	0.59	−1.00
Erichthonius brasiliensis	0.20	2.69	−0.87	0.18	0.30	−0.25	0.66	0.13	−0.66
Erichthonius sp. A	—	0.08	−1.00	—	—	—	0.66	3.75	−0.70
Exogone dispar	—	3.71	−1.00	—	0.47	−1.00	—	0.01	−1.00
Filograna implexa	—	20.42	−1.00	—	63.87	−1.00	—	21.90	−1.00
Luconacia incerta	—	3.27	−1.00	—	1.03	−1.00	—	0.18	−1.00
Malacoceros glutaeus	—	0.41	−1.00	—	0.81	−1.00	—	0.02	−1.00
Phyllochaetopterus socialis	—	0.21	−1.00	—	0.12	−1.00	—	12.40	−1.00
Pista palmata	—	0.09	−1.00	—	0.08	−1.00	—	8.60	−1.00
Podocerus sp. A	—	2.87	−1.00	0.18	0.27	−0.19	—	0.14	−1.00
Spiophanes bombyx	—	0.39	−1.00	—	0.46	−1.00	—	5.81	−1.00
Syllis spongicola	—	2.14	−1.00	—	1.90	−1.00	—	1.38	−1.00
Total	0.20	36.81		0.36	70.12		1.32	54.92	
Dominant species—stomachs									
Costoanachis avara	2.15	0.02	0.98	3.27	<0.01	0.99	—	—	—
Aspidosiphon gosnoldi	12.13	1.63	0.76	3.99	0.46	0.79	0.33	0.09	0.57
Glottidia pyramidata	0.20	0.01	0.88	—	0.01	−1.00	2.31	0.07	0.94
Iridopagurus dispar	—	—	—	0.36	0.01	0.97	4.29	0.07	0.97
Leptochela papulata	—	0.04	−1.00	2.54	0.09	0.93	0.33	0.12	0.46
Marginella hartleyanum	4.70	0.14	0.94	0.18	0.01	0.87	—	0.03	−1.00
Onuphis nebulosa	—	0.01	−1.00	—	0.05	−1.00	2.64	0.56	0.65
Osachila tuberosa	—	<0.01	−1.00	—	<0.01	−1.00	1.98	0.02	0.98
Pagurus carolinensis	2.35	0.40	0.71	4.36	0.30	0.87	2.97	0.07	0.96
Pargurus hendersoni	6.46	0.26	0.92	5.81	0.11	0.96	1.65	0.11	0.88
Total	27.99	2.51		20.51	1.05		16.50	1.14	

TABLE 4.—Percentage of similarity in diet (Bray-Curtis index) between sparid fishes collected from hard bottom habitats.

Species	*C. leucosteus*	*L. rhomboides*	*P. pagrus*	*S. aculeatus*
A. probatocephalus	0.182	0.369	0.125	0.207
C. leucosteus		0.053	0.264	0.060
L. rhomboides			0.037	0.249
P. pagrus				0.076

(*Aspidosiphon* spp.) were occasionally consumed by West Indian *Calamus*. Fishes of the genus *Calamus* have broad molariform teeth (Gregory 1933) that are used to crush the shells of gastropods, hermit crabs, and other invertebrates equipped with hard protective shells, and this is reflected in the food of *C. leucosteus* in the South Atlantic Bight. The motile gastropod shell is apparently a visual stimulus to whitebone porgy, which results in ingestion of the shell regardless of its inhabitant. Gastropods, hermit crabs, and sipunculids that were eaten consisted of very small species. All occupied similarly sized shells, and collumbellid shells (e.g., *Costoanachis avara* and *C. avara* shells occupied by other organisms) were the most frequently found shells in stomach samples.

Whitebone porgy demonstrated a relatively small change in food habits with increasing fish size. This is unusual for sparid fishes, many species of which switch between a herbivorous habit and an omnivorous or carnivorous habit during different life history stages (Christensen 1978; Ogburn 1984; Stoner and Livingston 1984; Darcy 1985a, b; Sedberry 1987). Many of these other sparids occupy grass beds or intertidal waters at certain life history stages and feed on tracheophytes and algae that are common on those shallow-water habitats. Whitebone porgy, like other sparids found in offshore habitats where algae are uncommon, do not feed on plant material (Manooch 1977; Sedberry 1983, 1987).

Most of the invertebrate species that dominated in benthic collections from the hard bottom habitat were not important in the diet of whitebone porgy. Most of these were polychaetes and amphipods that may have been too small to be consumed by a generalized predator like whitebone porgy; however, whitebone porgy probably does not forage directly on hard-bottom reef species, regardless of their size. Dominant prey species such as *Aspidosiphon gosnoldi*, *Glottidia pyramidata*, and *Onuphis nebulosa* are inhabitants of sandy bottoms (Wells and Gray 1964; Cutler 1973; Gardiner 1975; Cooper 1977; Fauchald and Jumars 1979), and *Leptochela papulata* is also commonly found in sandy habitats (Williams 1984).

Calamus leucosteus had a relatively high overlap in diet with *Pagrus pagrus* and *Archosargus probatocephalus*. Pagurid decapods and especially the barnacle *Balanus trigonus* were common in the diet of these three predators but were not consumed by the other sparids examined (South Carolina Wildlife and Marine Resources Department 1984). Aside from a sessile barnacle species, however, few other sessile organisms were consumed by whitebone porgy or red porgy. Red porgy fed mainly on motile decapods and fishes and can be classified as a generalized predator of motile organisms. *Archosargus probatocephalus* appeared to depend more on hard bottom habitat for feeding (Sedberry 1987); whereas, *Calamus leucosteus* fed on a combination of motile invertebrates and fishes, in addition to some hard bottom epifaunal species.

Stenotomus aculeatus had a low overlap in diet with whitebone porgy. Southern porgy, like whitebone porgy, are frequently taken in trawls over sand bottoms (Wenner et al. 1980), but they are not nearly as abundant as they are in hard bottom habitats (Sedberry and Van Dolah 1984). Southern porgy had a diet dominated by a pelecypod (*Ervilia concentrica*) and a cumacean (*Oxyurostylis smithi*) that are infaunal sand dwelling species (Van Engel 1972; Porter 1974); by planktonic species (copepods, *Calanopia americana*, and the caprellid *Phtisica marina*); and by an epifaunal amphipod (*Erichthonius brasiliensis*) that were rarely consumed by whitebone porgy (South Carolina Wildlife and Marine Resources Department 1984; this study). Since these two sparids feed heavily on sand dwelling benthos or near-bottom plankton, they are apparently not dependent on hard bottom habitat for food, although they are found in higher densities in hard bottom areas. Because they feed on different kinds of organisms (infaunal sedentary or planktonic species for southern porgy versus motile epifaunal species for whitebone porgy), there is little overlap in diet between these two species.

Overlap in diet between pinfish and whitebone porgy was very low. Pinfish examined in the present study ate primarily a hard-bottom, sessile, tube-dwelling amphipod, *Erichthonius brasiliensis*, (36% of prey items) that was rarely consumed by whitebone porgy. Pinfish are apparently more closely associated with substrates from which they can browse on attached organisms, as has been noted in previous studies (Stoner and Livingston 1984). Because pinfish fed on attached epifauna, this species was similar in diet to sheepshead, a heavy grazer on attached epifauna (Sedberry 1987). Whereas *Calamus* spp. possess conical teeth in the anterior of the jaws for grasping motile prey and strong molariform teeth on the sides for crushing shells (Gregory 1933; Randall and Caldwell 1966; Randall 1967), the anterior of the jaws of pinfish

are provided with incisors that are suited to scraping epifauna (Stoner and Livingston 1984).

Predation by fishes and other organisms can be an important factor in regulating the structure of sessile invertebrate communities (Peterson 1979; Sedberry 1987); however, it is obvious from the present results that whitebone porgy have little impact on hard-bottom epifaunal communities. While they are an abundant and a dominant member of the predatory fish community (Sedberry and Van Dolah 1984), whitebone porgy do not function as keystone predators (Paine 1969) in hard bottom reefs of the South Atlantic Bight.

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A Photographic Survey of the Megafauna of the Central and Eastern Gulf of Maine

Richard W. Langton and Joseph R. Uzmann

ABSTRACT: During the summers of 1983 through 1985 the JOHNSON-SEA-LINK manned submersible systems were used to survey the megafauna in the central and eastern Gulf of Maine. Quantitative 35 mm color photographs were taken at 29 stations, 5,714 photos were examined, and the megafauna identified. Eighteen taxa represented 96% of all the organisms counted, and of these 18 only 5 groups, from 2 phyla, were numerically dominant. Ophiuroidea and Asteroidea were the dominant echinoderms while Ceriantharia, *Pennatula*, and *Bolocera* were the dominant cnidarians. The relationship between sediment type and the megafauna was also investigated. Again, relatively few taxa were important and these groups showed substrate specificity. *Pennatula* occurred in a variety of substrates but were most abundant in silt (1.20 individuals m^{-2}). Ceriantharians were generally found in sandy substrates at densities as high as 1.12 m^{-2}, while *Bolocera* dominated on gravel but at much lower densities (0.017 m^{-2}). Scallops, *Placopecten*, were restricted to gravelly sand, while pandalid shrimp occurred on the finer sands and mud, both at low densities ($\leq$0.04 m^{-2}). Asteroidea covered almost the entire range of substrates at low density, although they were more numerous on sands (max. = 0.16 m^{-2}) and gravels (max. = 0.17^{-2}). Ophiuroidea reached their maximum density (1.23 m^{-2}) on slightly gravelly sand but also occurred at $\geq$1 m^{-2} on gravelly mud. The only fish observed at $\geq$0.01 m^{-2} were *Lumpenus lumpretaeformis* and *Merluccius bilinearis*, both of which were found on mud substrates.

The Gulf of Maine has been described as an epicontinental sea or macroestuary extending from Massachusetts to Nova Scotia (Uchupi 1965, 1966; Emery and Uchupi 1972; Campbell 1986). It has its origins in the last glacial period, 11,000 BP (Before Present), having been shaped by both fluvial and glacial erosion (Emery et al. 1965; Ziegler et al. 1965). The resulting uneven topography and mixture of sediments offer a variety of habitats for the establishment of benthic organisms, of both commercial and noncommercial value (Rich 1929; Emery et al. 1965). The distribution and abundance of commercial species have been studied over the years (Bigelow and Schroeder 1939, 1953) but with few exceptions, primarily small-scale studies, the benthic communities have received little attention (Dexter 1944; Stickney 1959; Hanks 1964; Sears and Cooper 1978; Larsen 1979; Hulbert et al. 1982; Larsen et al. 1983a, b; Witman and Cooper 1983). Published reports describing the soft bottom benthos in the offshore regions of the Gulf are limited to the work of Emery et al. (1965), who conducted a geological and biological survey of the U.S. east coast continental shelf, and a study of two contiguous deep basins (Wilkinson and Murray) in the western Gulf by Rowe et al. (1975). Several, as yet unpublished, databases also exist describing the Gulf's benthic communities. One of these is a detailed expansion of the work outlined by Emery et al. (1965) (Theroux and Wigley[1]), while the other is from recent box core sampling and submersible observations in the Gulf (Watling et al. 1988).

The current study was initiated as a submersible survey of offshore lobster habitat in the Gulf of Maine. In addition to this fisheries orientation, however, numerous 35 mm color photographs were taken to characterize the associated megafauna. Because of the paucity of information on the benthic communities of the Gulf, it is the purpose of this paper to summarize the photographic data collected from the years 1983 through 1985 using the JOHNSON-SEA-LINK submersible systems.

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[1]Theroux, R. B., and R. L. Wigley. Quantitative composition and distribution of the macrobenthic invertebrate fauna of the New England region. Unpubl. manuscr. Northeast Fisheries Center, Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

METHODS

During the summers of 1983 through 1985, the JOHNSON-SEA-LINK manned submersible systems were used to survey the megafauna at 29 stations in the Gulf of Maine (Fig. 1; App. Table 1). In 1983, locations in the outer Gulf, Georges Basin and the area northward toward Truxton Swell, were sampled; in 1984, the stations in the middle of the Gulf and Jordan Basin were visited. In 1985, a series of stations running from the center of Jordan Basin to the northeast towards the Bay of Fundy were to be sampled. Unfortunately, weather limited available diving time in 1985 and forced diving operations inshore toward the Nova Scotian coast after only three stations were sampled. The purpose of the study was to document offshore lobster habitat; therefore, dive site selection was based on commercial trap fishery information as well as on National Marine Fisheries Service data from their biannual groundfish trawl surveys of lobster catches.

Submersible dives at each station followed a standard protocol, with the diver-scientist recording observations on a cassette tape or video camera as well as collecting surficial sediment samples over the course of a transect. In addition to these data, 35 mm color photographs were taken automatically at 10 to 15 s intervals throughout the dive.

In the laboratory, a minimum of 200 randomly chose photographs from each dive, or all photos taken during the entire dive if <200 frames total, were individually examined and the megafauna identified and enumerated. The

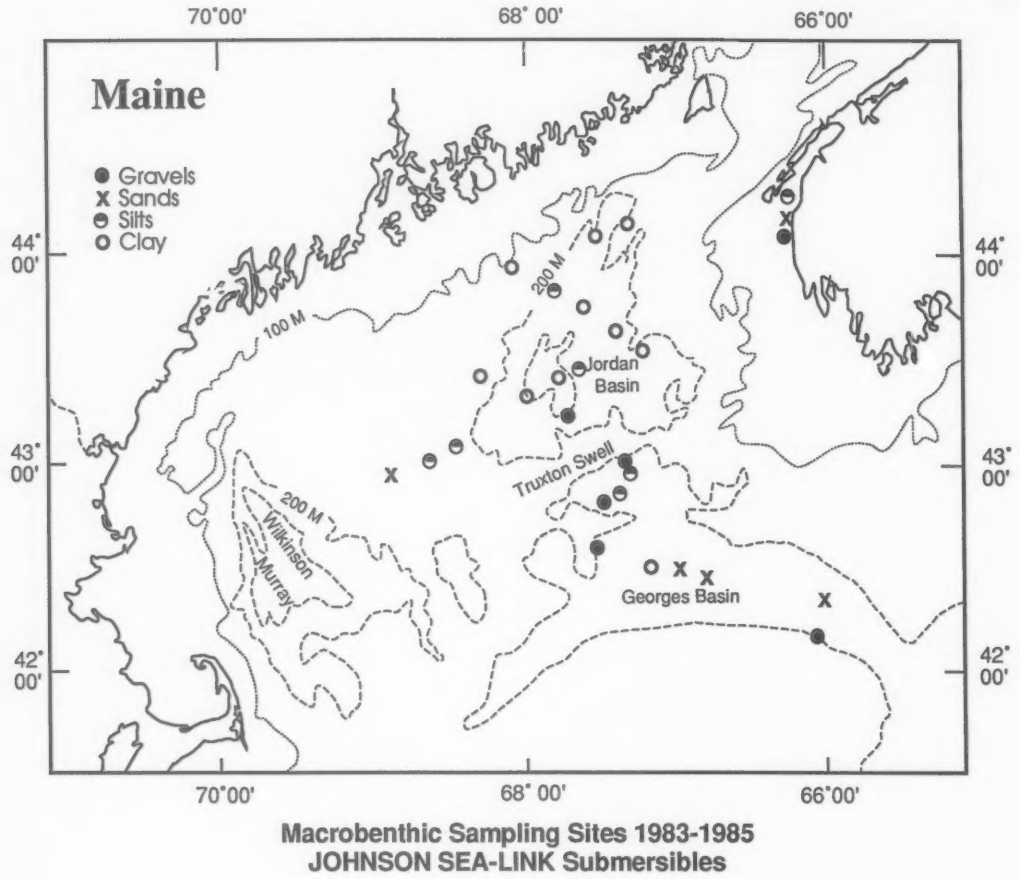

FIGURE 1.—Dive site locations for 29 dives constituting the megafaunal survey, 1983–85, using the JOHNSON-SEA-LINK submersible systems.

categories of megafauna, representing a variety of taxonomic levels, that could be resolved in the photographs are listed in Appendix Table 2. From one to seven sediment samples, collected on each dive, were analyzed by the U.S. Geological Survey for surficial grain size analysis. The statistical parameters for this analysis were calculated by the method of moments (Krumbein and Pettijohn 1938), while the average sediment types for each dive were classified and are described using the terminology of Folk (1980).

RESULTS

Sediment types are shown in Figure 1 at the 29 dive locations. The general sediment pattern, from south to north, is a gradation of coarse to fine sediments. Georges Basin is, generally, sandy along its midsection, changing into a gravelly area towards Truxton Swell. Jordan Basin, which is north of Georges Basin, is dominated by finer silts and clays.

A total of 5,714 color photographs (35 mm slides) were examined from the 29 submersible dives. Over 27,000 individual organisms were counted. The overall taxonomic ranking, based on the percentage of total numbers observed for the top 18 taxonomically distinct groups, is shown in Figure 2. These 18 groups represent 96% of all the organisms counted. From the figure, it is clear that there are only five numerically dominant taxa representing two phyla, the Echinodermata and the Cnidaria. Ophiuroidea and Asteroidea are the dominant echinoderms, while ceriantharian anemones, sea pens of the genus *Pennatula*, and rock (*Bolocera*) anemones account for the dominant cnidarians.

If the same data are examined on a year and location basis, there are, again, very few dominant groups. In addition to the echinoderms and cnidarians observed in all three years, arthropods (pandalid shrimp) were reasonably abundant in 1984 in the middle Gulf and southern Jordan Basin area, while invertebrate tubes (polychaetes or amphipods) occurred at the stations, visited in 1985, in central Jordan Basin and to the northeast (Table 1). The year and area breakdown, like the overall ranking, demonstrates a simple picture for the softer sediment megafaunal communities in the Gulf of Maine. Seven taxonomically distinct groups account for 97 to 99% of all the biota observed.

The relation between sediment type and animal abundance is shown in Figure 3 and detailed in Appendix Table 1. Of interest is the substrate specificity of the various groups. Sea pens, *Pennatula* (most likely *P. aculeata*, Langton, pers. obs.), occurred in clay and silts as well as gravel. They were, however, most common in silt reaching a maximum density of 1.20 animals m^{-2}. They occurred in gravel at only 2 stations compared to 10 stations with

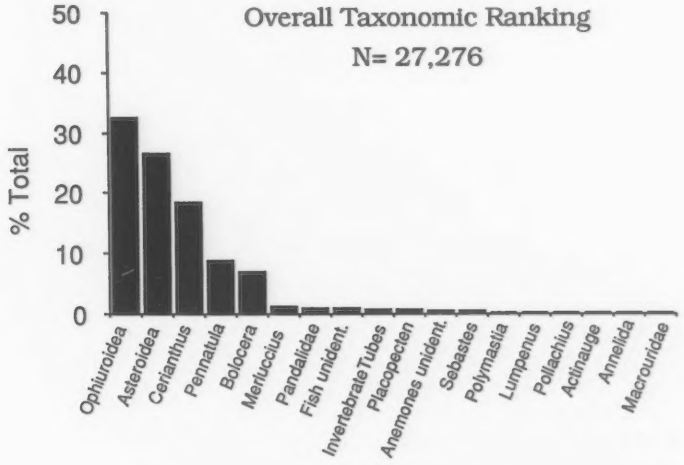

FIGURE 2.—Overall taxonomic ranking, expressed as percentage of the total number of organisms observed (N = 27,276), for 29 submersible dives in the Gulf of Maine from 1983 through 1985.

TABLE 1.—Breakdown of the major groups of benthic organisms, expressed as the percentage of number of total organisms observed, for each of the three years of the survey. These seven groups account for 97 to 99% of all megafaunal animals observed in the areas surveyed for any given year.

	% of major groups by year and location		
Groups	1983 Georges Basin Truxton Swell	1984 Mid-Gulf, Southern Jordan Basin	1985 Central Jordan Basin to the northeast
Pennatula	38.0	28.0	4.0
Cerianthus	38.3	5.0	10.3
Bolocera	10.1	–	1.3
Invertebrate tubes (Polychaete or Amphipod)	–	–	2.1
Pandalidae	–	1.2	–
Asteroidea	6.5	2.5	11.5
Ophiuroidea	2.8	62.2	67.9
Total %	97.5	98.9	97.1

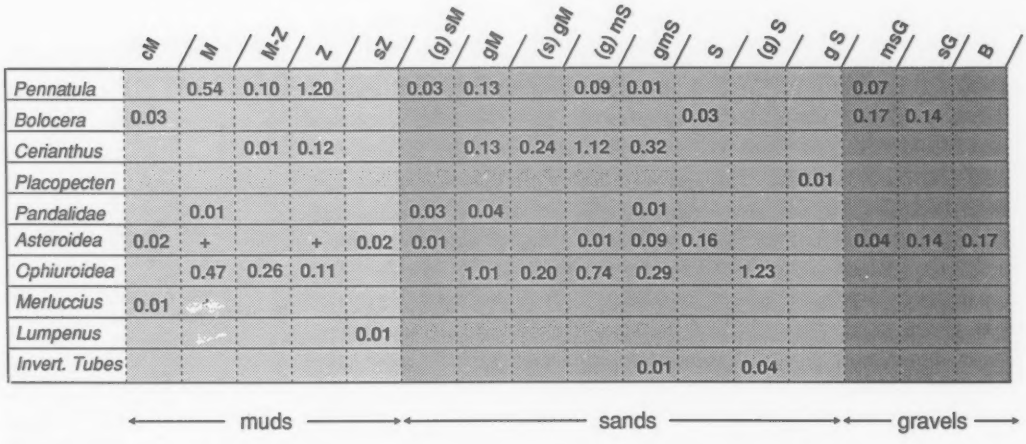

FIGURE 3.—Occurrence of dominant megafaunal groups associated with substrate type. Data is expressed as numbers of individuals per square meter of bottom for each sediment type. Only taxa that had a density of ≥0.01 animals per squre meter in any one sediment type are included in the figure. The actual density is given when it equals or exceeds the 0.01 value while a "+" indicates presence but at a density of <0.01 animal per square meter. The sediment types follow the terminology of Folk (1980) and are cM = clayey mud, M = mud, M-Z = Mud-Silt, Z = Silt, sZ = sandy silt, (g)sM = slightly gravelly sandy mud, gM = gravelly mud, (s)gM = slightly sandy gravelly mud, (g)mS = slightly gravelly muddy sand, gmS = gravelly muddy sand, S = sand, (g)S = slightly gravelly sand, gS = gravelly sand, msG = muddy sandy gravel, sG = sandy gravel, and B = boulder field.

clay and silt substrates. *Cerianthus* sp. (probably *C. borealis*, see Shepard et al. 1986), a burrowing anemone, was also not especially substrate specific. It was found over the entire gradation of sandy substrates as well as some of the silts, although it reached its highest density (1.12 m^{-2}) in slightly gravelly muddy sand. *Bolocera tuediae*, on the other hand, is an anemone that attaches to hard, rocky, substrates. Consequently, it was observed in areas of gravel and sand at a maximum density of 0.17 m^{-2}. On the sandy substrates, these anemones, as well as the few animals observed on clayey mud, were often found attached to a rock outcrop or loose boulder rather than directly to the finer sediment. The sea scallop, *Placopecten magellanicus*, was restricted to gravelly sand while pandalid shrimp occurred on finer sands and muds; both at relatively low densities, 0.01 and ≤0.04 m^{-2}, respectively. Asteroidea which include a variety of genera (e.g., *Asterias*, *Hippasteria*, *Henricia*, *Cros-*

saster, and *Solaster*) occurred over virtually all substrate types but were more prevalent on coarser sediments, reaching a maximum density of 0.17 m^{-2} in a bouldery area. In contrast, Ophiuroidea did not occur on gravel substrates in significant numbers but did occur on slightly gravelly sand at high density (1.23 m^{-2}) as well as on the finer sands and muds. Only two fish species occurred in sufficient density to demonstrate any substrate specificity. The silver hake, *Merluccius bilinearis*, was observed resting on the bottom on fine mud sediments, while the snake blenny, *Lumpenus lumpretaeformis*, was observed on sandy silt.

DISCUSSION

This study is the first, broad scale, megafaunal survey in the Gulf of Maine using manned submersibles. Previous submersible work was limited to four DSRV *Alvin* dives in Wilkinson and Murray Basins in 1971 and 1972, described by Rowe et al. (1975). The study by Rowe et al. reported that pandalid shrimp and ophiuroids were the numerically dominant megafaunal animals observed along several transects in these basins. From the present work, it is clear that ophiuroids are numerically dominant throughout the central and eastern Gulf on the finer sediments (Figs. 2, 3). Pandalid shrimp, on the other hand, ranked only seventh in abundance in the present work (Fig. 2). Perhaps the abundance of shrimp observed by Rowe et al. (1975) reflected the high population levels, and correspondingly high catches, of *Pandalus borealis* that occurred in the Gulf of Maine in the late 1960s and early 1970s (Shumway et al. 1985).

The description of the megafauna in the Gulf of Maine that emerges from this study is not complex. Relatively few taxa, or taxonomic groups, from two phyla dominated the megabenthos on a numerical basis (Fig. 2; App. Table 1). These two phyla (Echinodermata and Cnidaria) are different from the dominants identified from macrobenthic surveys in the Gulf, as might be expected, owing to the methodological differences and scales of resolution. Theroux and Wigley (fn. 1), for example, reported molluscs, annelids, and crustaceans to be the numerical dominants, based on a more extensive and geographically restricted analysis of the Emery et al. (1965) survey, using surface deployed sampling gear. Watling et al. (1988) identified annelids, crustaceans, and echinoderms as the numerically dominant groups based primarily on surface deployed box core samples. Neither ceriantharians nor pennatulids, the numerical dominants in this study, are adequately sampled with a 0.1 m^2 box core (Watling[2]). Rowe et al. (1975) also noted significant differences between core samples and visual counts, while other studies specifically comparing submersibles and photographic transects with other sampling gear have shown substantial differences when conducting a faunal census (Wigley and Theroux 1970; Uzmann et al. 1977; Theroux 1984).

The distribution of megafaunal animals is related to sediment type in the Gulf of Maine (see Figure 3 and Appendix Table 1). Watling et al. (1988) also identified substrate, together with the temperature range of the overlying water mass, as major factors resulting in seven discrete macrobenthic species assemblages in the Gulf of Maine. Their analysis is based on both box core and submersible sampling. Zoogeographic studies on specific megafaunal components in the Gulf of Maine are rare, only three taxonomic groups occurring in this geographic region have been investigated (Wigley 1960; Haynes and Wigley 1969; Franz et al. 1981; Shepard et al. 1986). In these three instances the various environmental factors, including sediment type, that potentially control the animals distributional patterns have been examined. Shepard et al. (1986), for example, completed an extensive study of Ceriantharia off the northeast coast of the United States. Geographic and bathymetric zonation was attributed primarily to temperature and secondarily to food supply and sediment type. They found *Cerianthus* to be tolerant of a wide range of temperature (8°–16°C) and to occur on most substrates except gravel and coarse shifting sand. In the present study ceriantharians were also found to have little substrate fidelity although there was a noticeable absence from areas of boulders and gravel (Fig. 3). Pandalid shrimp, on the other hand, have been shown to have a stronger affinity for sediment type (Wigley 1960). Unfortunately the species of shrimp could not be identified in the photographs we examined so a detailed comparison with Wigley's results on the four species of Pandalidae occurring in the Gulf of Maine is not possible. Nevertheless, Haynes and Wigley

[2]L. Watling, Darling Marine Center, University of Maine, Walpole, ME 04573, pers. commun. 1988.

(1969), as well as Bigelow and Schroeder (1939) in an earlier study, have both noted a strong affinity between organically rich sediment and the occurrence of the Gulf's largest pandalid, *Pandalus borealis*. The observed occurrence of shrimp in our photographs corresponds to substrates containing silt and, generally, finer grained materials (Fig. 3), thus, once again, confirming the relationship between pandalid shrimp and, presumably, high organic sediments in the Gulf of Maine. In the last of the three groups, for which there is information relating distributional patterns to the environment, Franz et al. (1981) identified temperature as the major controlling factor of asteroid distribution. Their study identified 15 different species of seastar in the Gulf of Maine which they assigned to 3 zoogeographic groups. These species have a variety of substrate requirements. In our study temperature varied little between dive locations, depth, and year (App. Table 1), whereas sediment type did. This variation in substrate is reflected in Figure 3 where asteroids are shown to occur on almost all sediment types. Although sediment type is obviously not the only factor that determines a species occurrence, it is important when considering the patterns of species distribution throughout the Gulf of Maine and should be evaluated on a species specific level.

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APPENDIX TABLE 1.—Summary of data for 29 submersible dives conducted using the JOHNSON-SEA-LINK submersible systems from 1983—85 in the Gulf of Maine. Mean percentage of sediment composition categories: G = gravel; SA = sand; SI = silt; CL = clay. "Most abundant animals" includes any group where 10 or more individuals were counted in the photographs from each dive.

Date (Mo/day)	JSL I or II Dive #	Dive location Lat. N	Dive location Long. W	Max. depth (m)	Bottom temp. (°C)	Sediment $\bar{x}$% composition G SA SI CL	No. of sediment samples	Most abundant animals (#m^{-2})
1983								
8/3	1407	42°58.48′	67°31.18′	226	8.8	0/46/35/19	1	0.024 *Bolocera* 0.023 Asteroidea 0.005 *Merluccius* 0.004 Fish unid.
8/3	1408	42°58.48′	67°31.18′	229	8.7	0/33/44/23	1	0.030 *Bolocera* 0.013 Asteroidea 0.012 *Merluccius*
8/4	1409	43°01.30′	67°32.12′	201	8.8	38/45/12/5	4	0.214 *Pennatula* 0.044 *Bolocera* 0.028 Asteroidea
8/4	1410	43°04.12′	67°43.24′	153	8.2	36/50/10/4	3	0.115 *Bolocera* 0.047 Asteroidea 0.008 *Polymastia*
8/5	1413	42°45.18′	67°37.30′	206	8.9	44/45/8/3	5	0.346 *Bolocera* 0.043 Asteroidea 0.021 *Pollachius*
8/6	1414	42°28.18′	67°20.06′	323	8.7	0/5/64/31	2	2.408 *Pennatula* 0.243 *Cerianthus* 0.008 Macrouridae 0.007 Asteroidea
8/6	1415	42°26.24′	67°07.36′	381	8.6	5/41/37/17	5	0.238 *Cerianthus* 0.204 Ophiuroidea
8/7	1416	42°08.30′	66°09.00′	177	8.1	61/38/<1/<1	4	0.085 *Bolocera* 0.013 Asteroidea
8/8	1418	42°14.30′	66°09.00′	264	7.3	10/89/<1/<1	7	0.010 *Placopecten*
8/8	1419	42°23.42′	66°52.48′	351	7.9	4/52/26/18	5	2.234 *Cerianthus* 0.179 *Pennatula* 0.010 Asteroidea
8/10	1422	42°32.00′	67°38.00′	171	8.7	38/53/<1/2	5	0.254 Asteroidea 0.201 *Bolocera*
1984								
7/17	880	42°51.31′	68°54.04′	144	6.9	13/68/13/6	2	0.327 *Cerianthus* 0.182 Asteroidea 0.009 *Sebastes*
7/18	881	42°58.11′	68°44.25′	205	7.3	3/32/39/26	3	0.034 Pandalidae 0.032 *Pennatula* 0.010 Asteroidea
7/18	882	43°03.16′	68°32.43′	181	7.0	7/29/39/25	3	1.009 Ophiuroidea 0.126 *Pennatula* 0.125 *Cerianthus* 0.039 Pandalidae

APPENDIX TABLE 1.—*Continued.*

Date (Mo/day)	JSL I or II Dive #	Dive location Lat. N	Dive location Long. W	Max. depth (m)	Bottom temp. (°C)	Sediment $\bar{x}$ % composition G SA SI CL	No. of sediment samples	Most abundant animals (#m^{-2})
1984—*Continued*								
7/19	883	43°48.31′	67°54.22′	174	7.3	0/<1/64/36	1	2.418 *Pennatula* 0.021 *Merluccius* 0.017 Pandalidae
7/19	885	43°20.55′	68°24.46′	194	7.8	0/<1/56/44	3	0.973 Ophiuroidea 0.302 *Pennatula* 0.009 Pandalidae
7/20	887	43°17.45′	67°55.44′	231	7.9	0/<1/57/43	3	0.594 Ophiuroidea 0.116 *Pennatula* 0.012 Pandalidae
7/20	888	43°22.32′	67°43.52′	270	8.1	0/<1/58/42	3	0.555 Ophiuroidea 0.214 *Pennatula*
7/21	889	43°54.01′	68°05.32′	180	7.4	0/<1/60/40	2	0.603 *Pennatula* 0.025 Asteroidea
7/21	890	43°43.01′	67°43.06′	236	9.2	0/<1/56/44	2	1.183 Ophiuroidea 0.019 Invert. tubes
7/21	891	43°37.26′	67°31.29′	227	8.3	0/<1/69/31	2	0.221 Ophiuroidea
7/22	892	43°27.19′	67°31.48′	224	8.0	3/19/53/26	2	1.472 Ophiuroidea
7/22	893	43°30.27′	67°18.35′	220	9.2	0/7/59/34	2	0.123 *Pennatula*
1985								
6/25	1093	43°58.14′	67°26.52′	187	7.9	15/37/36/12	3	0.584 Ophiuroidea 0.304 *Cerianthus* 0.027 Invert. tubes 0.021 *Pennatula* 0.011 Pandalidae
6/25	1094	44°04.22′	67°35.45′	201	8.2	0/2/65/32	1	0.260 Ophiuroidea 0.096 *Pennatula* 0.009 *Cerianthus*
6/26	1095	44°08.13′	67°26.52′	242	8.9	1/7/61/31	4	1.225 Ophiuroidea 0.037 Invert. tubes 0.
6/27	1096	44°16.13′	66°16.47′	52	9.1	0/39/55/6	1	0.021 Asteroidea 0.011 *Lumpenus*
6/27	1097	44°09.52′	66°13.37′	23	8.7	<1/97/2/<1	1	0.156 Asteroidea 0.026 *Bolocera*
6/28	1098	44°03.28′	66°13.57′	18	9.6	boulders	—	0.169 Asteroidea

APPENDIX TABLE 2.—Listing of the categories of megafauna that could be resolved and identified in the 35 mm photographs. The actual area of sea floor photographed in each frame was 7.0 m^2.

- Macrophytes
- Porifera
  - Orange colonial forms
  - White colonial forms
  - Yellow colonial forms
  - Stalked sponges
  - Sponge, unidentified
  - *Polymastia*
- Cnidaria
  - Hydroids
  - *Tubularia*
  - *Pennatula*
  - *Bolocera*
  - *Actinauge*
  - *Cerianthus*
  - Anemones, unidentified
- Brachiopoda
- Mollusca
  - Gastropoda (Welks)
  - *Placopecten magellanicus*
- Annelida
  - Invertebrate tubes (Polychaete or Amphipod)
- Arthropoda
  - Pandalidae
  - *Homarus americanus*
  - *Pagarus* sp.
  - *Cancer* sp.
- Echinodermata
  - Echinoidea
  - *Echinarachnius parma*
  - Asteroidea
  - Ophiuroidea
- Vertebrata
  - *Myxine glutinosa*
  - *Omochelys cruentifer*
  - *Merluccius bilinearis*
  - *Gadus morhua*
  - *Melanogrammus aeglefinus*
  - *Pollachius virens*
  - *Urophycis* sp.
  - *Brosme brosme*
  - Macrouridae
  - Flatfish
  - *Sebaster fasciatus*
  - *Myoxocephalus* sp.
  - *Aspidophoroides monopterygius*
  - *Lumpenus lumpretaeformis*
  - Blenny, unidentified
  - *Leptoclinus maculatus*
  - *Macrozoarces americanus*
  - *Lophius americanus*
  - Fish, unidentified

Submersible Observations of Deep-Reef Fishes of Heceta Bank, Oregon

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W. H. Barss, and R. M. Starr

ABSTRACT: Rockfishes, *Sebastes* spp., were the most numerous and speciose fishes seen during 16 submersible dives from 64 to 305 m depth in the vicinity of Heceta Bank off the coast of Oregon. Dense schools of juvenile rockfishes and large yellowtail rockfish, *S. flavidus*, were observed only over rocky, high relief areas near the top of the bank, and highest densities of small benthic rockfishes (up to 5–10/m^2) on the flanks of the bank. These observations suggest that shallow, rocky portions of Heceta Bank are a nursery area for juvenile rockfishes. Two species groups of nonschooling fishes were identified based on transects over the diverse seafloor habitats around the bank: one comprised primarily of rockfishes in shallow water on rock and cobble, and the other comprised of flatfishes, agonids, sablefish, and some rockfishes in deep water over mud and cobble. Species composition of fishes observed from submersible dives differed from species composition of fishes taken from trawl catches in the same general areas.

Prominent offshore submarine banks of exposed bedrock, formed by subduction of oceanic plates, occur along the continental shelf of western North America (Kulm and Fowler 1974), providing a specialized habitat for marine fauna. Large aggregations of rockfishes (Scorpaenidae: *Sebastes*) and other fishes are often associated with these banks (Isaacs and Schwartzlose 1965), just as concentrations of fishes are found on or over seamounts in the North Pacific Ocean (Uda and Ishino 1958; Uchida and Tagami 1985; Uchida et al. 1986).

Heceta Bank, located about 55 km off the central Oregon coast, rises abruptly from depths of over 1,000 m on its seaward face to depths of <60 m (Figs. 1, 2). Trawlable areas around Heceta Bank support a large portion of Oregon's commercial fishery production. The bank itself is thought to be a nursery for juvenile fishes. Several surveys of near-bottom fishery resources of the region have been attempted using bottom trawls (Gunderson and Sample 1980; Barss et al. 1982; Weinberg et al. 1984). However much of the bank is too rugged for bottom trawling, and until our study, no submersible surveys of this area had been made. Thus, species composition, abundances, and distributions of fishes on Heceta Bank itself are largely unknown.

We used a manned submersible to conduct surveys of fishes on and around Heceta Bank. Our goals were to assess visually the abundances of fishes on Heceta Bank, to relate distributions and species assemblages with habitat type and depth, and to evaluate the importance of the bank as a nursery and refugium for commercially important fishes.

METHODS

We dove 16 times in the vicinity of Heceta Bank (Fig. 2) during daylight on 23–31 August 1987, using the submersible *Mermaid II*. Bottom depths ranged from 64 to 305 m. Usually two or three visual belt transects were made during each dive. During each transect the position of the submersible and the distance traversed in 30 minutes at speeds of 1.5–2.0 km/h were determined from Loran C fixes by the surface vessel *Aloha* as it followed a surface buoy towed by the submersible. In this paper we report on 21 transects from 10 dives in which the submersible attempted to follow a compass course parallel to isobaths. Two scientists and a pilot were on each dive. Scientists switched positions from the bow window to a stern jump seat between 30 min transects. Seven scientists made dives.

All fishes seen between two fixed points on the submersible's bumper (a path about 3.5 m wide

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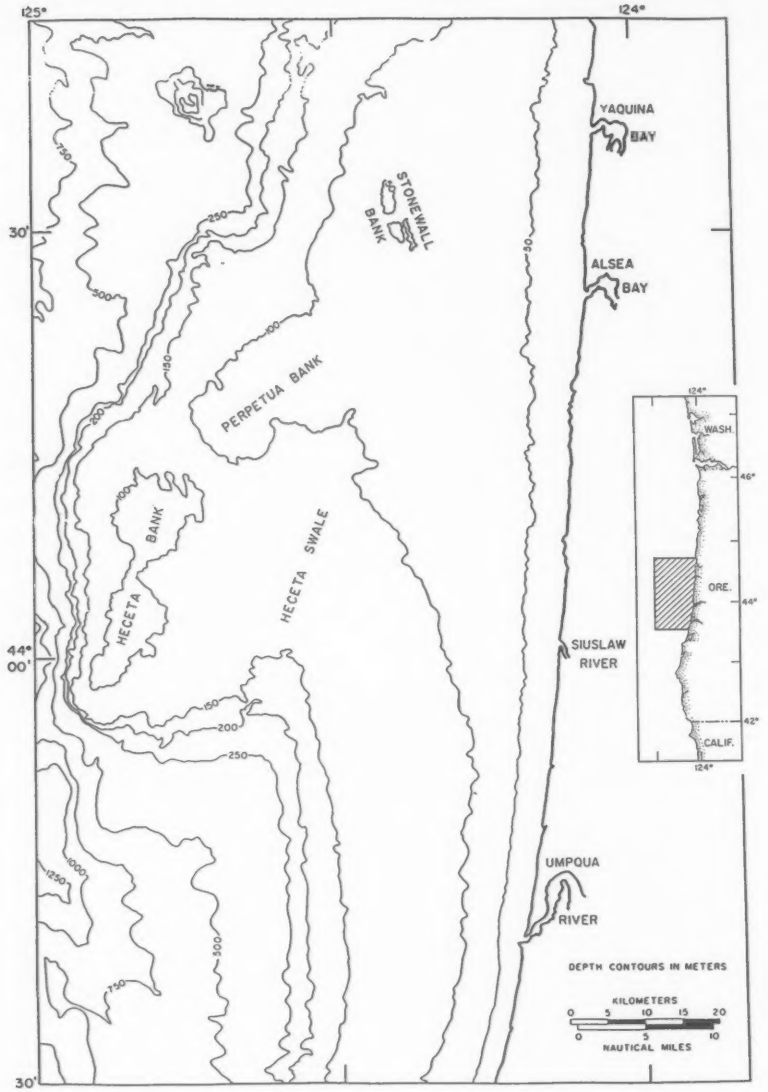

FIGURE 1.—Chart of the central Oregon coast showing Heceta Bank (depth in meters), and insert showing area covered by chart.

on the bottom at an altitude of 2 m) were identified when possible, counted, and lengths estimated to the nearest 10 cm. These data were simultaneously recorded on tape recorders and/or an event recorder by one of the two scientists on each dive. Altitude above the bottom was determined by observing a length of chain marked in decimeters suspended below the submersible and visible from the port. Altitude was fairly constant, about 2 m, on dives over uniform bottom. A fiberglass "T"-shaped rod, protruding 2.5 m from the bow of the submersible with black and white bands at 10 cm intervals, and a similar 50 cm bar with 10 cm bands attached to the bottom of the chain were used to estimate fish lengths.

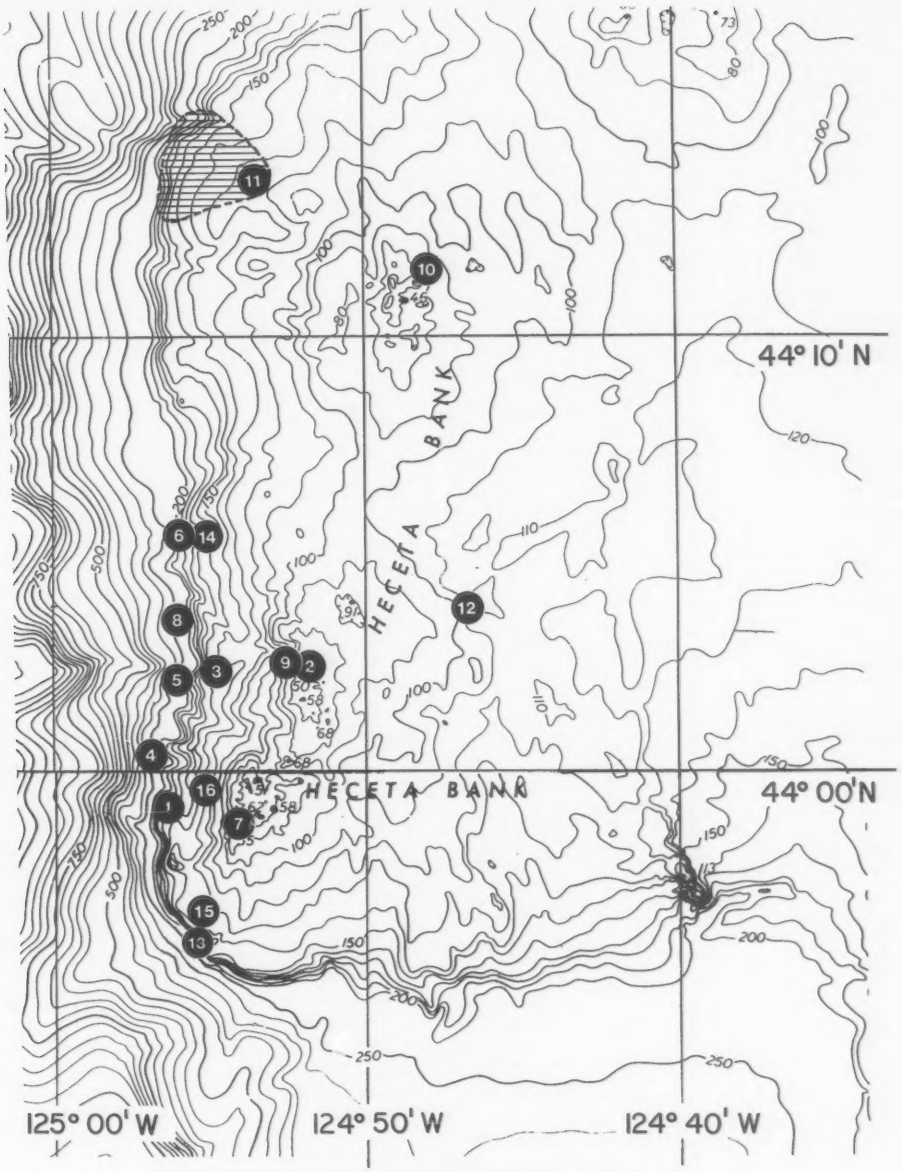

FIGURE 2.—Location of the 16 dives on Heceta Bank. Hatched areas indicate locations of bottom trawling.

External lighting consisted of two 500 W and two 150 W iodide lamps. A Photo-Sea 1000[1] 35 mm camera with strobe and a CM-55 Underwater Television Camera were used on every dive to assist in identification of fishes after the dives. We used a slurp gun and rotenone dispenser (Straty 1987) to collect voucher specimens. Between transects on some dives the submersible rested on the bottom with lights and

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

thrusters off for about 10 minutes. The lights were then turned on to determine their effects on fish behavior. Although "marine snow" was sometimes dense, visibility near the bottom was 3–5 m on all dives. Observations were sometimes made with ambient light from the submersible's conning tower at shallow depths.

A hierarchical cluster analysis (see Pimentel 1979), using presence or absence of species, was used to determine the similarity of nonschooling fish assemblages among transects. Schooling fishes were not included because most were small and could not be accurately enumerated or identified to species.

RESULTS

We encountered diverse and patchy substrates. Bottom types ranged from soft mud to rock walls and pinnacles. The bottom was often mud at depths below about 150 m, and cobble or rock at shallower depths. Massive rock formations, often sculptured into ridges and valleys, existed at depths of 75 m or less. Although habitats were generally stratified by depth, bottom type typically varied within a dive.

We observed a total of 42 taxa of fishes, including 31 identified species (Table 1). Rockfishes (Scorpaenidae) were by far the most abundant and speciose group: 12 species of *Sebastes* were identified. Of the nonschooling fishes, small "blotched" rockfishes, tentatively identified as sharpchin rockfish, *S. zacentrus*, were seen more frequently on transects of contour dives than all other fishes combined (Table 1). Rockfishes ranked first in abundance on 15 transects and second in abundance on 10 of the 21 transects (Table 2). The most numerous of the identified nonschooling species was the rosethorn rockfish, *Sebastes helvomaculatus*. The most numerous of the identified schooling species was yellowtail rockfish, *S. flavidus*; sometimes nonschooling individuals of this species were seen.

TABLE 1.—Rank order of abundances of nonschooling fishes seen on the 21 transects on Heceta Bank.

Nonschooling fishes	Total no. observed
Sharpchin rockfish, *Sebastes zacentrus?*	949
Unidentified small rockfish	902
Rosethorn rockfish, *Sebastes helvomaculatus*	409
Zoarcidae	164
Sablefish, *Anoplopoma fimbria*	140
Pygmy rockfish, *Sebastes wilsoni?*	132
Slender sole, *Lyopsetta exilis*	99
Dover sole, *Microstomus pacificus*	97
Unidentified large rockfish	71
Agonidae	67
Greenstriped rockfish, *Sebastes elongatus*	55
Unidentified flatfish	52
Cottidae	51
Hagfish	40
Shortspine thornyhead, *Sebastolobus alascanus*	33
Slim sculpin, *Radulinus asprellus*	33
Rex sole, *Glyptocephalus zachirus*	33
Splitnose rockfish, *Sebastes diploproa*	32
Yelloweye rockfish, *Sebastes ruberrimus*	25
Canary rockfish, *Sebastes pinniger*	25
Kelp greenling, *Hexagrammos decagrammus*	23
Unknown fish	21
Darkblotched rockfish, *Sebastes crameri*	19
Yellowtail rockfish, *Sebastes flavidus*	16
Lingcod, *Ophiodon elongatus*	14
Spotted ratfish, *Hydrolagus colliei*	12
Longnose skate, *Raja rhina*	10
Blenniidae	8
Bathymasteridae	8
Rajidae	7
English sole, *Parophrys vetulus*	7
Redbanded rockfish, *Sebastes babcocki*	7
Arrowtooth flounder, *Atheresthes stomias*	6
Big skate, *Raja binoculata*	4
Pacific hake, *Merluccius productus*	4
Tiger rockfish, *Sebastes nigrocinctus*	2
Wolf-eel, *Anarrhichthys ocellatus*	2
Sand sole, *Psettichthys melanostictus*	2
Stripetail rockfish, *Sebastes saxicola*	1
Ragfish, *Icosteus aenigmaticus*	1
Sand dab, *Citharichthys* sp.	1
Threadfin sculpin, *Icelinus filamentosus*	1
Osmeridae	1
Greenspotted rockfish, *Sebastes chlorostictus*	1

Assemblages of Nonschooling Fishes

Cluster analysis grouped the nonschooling fishes into two major groups associated with two major habitat types and two depth zones—bottoms where rock and cobble predominated at depths of 67–145 m (Habitat I:13 transects) and mud and cobble bottoms at depths of 140–299 m (Habitat II:8 transects) (Fig. 3, Table 2). Two subclusters occurred within each habitat group at a Euclidian distance of <0.4. The distance (dissimilarity) between the two major habitat types was almost twice as great as among the four subclusters. As can be seen in Table 2, differences in species compositions among clusters were not large. Many species were found in several habitat/depth types. Distinct species assemblages were not obvious. The four habitat groups were as follows:

IA-Shallow Rock Habitat. Six transects near the top of the bank (67–76 m) were over a seafloor predominated by high-relief, massive rock walls often separated by eroded valleys filled with cobble or sand. Four transects were over cobble and flat rock interspersed with patches of mud at depths of 104–149 m. Crinoids (*Florometra serratissima*), sponges, anemones (*Metridium* sp.), hydrocorals, and bryozoans were abundant on exposed rock faces. Basket stars (*Gorgonocephalus* sp.) were obvious on ridge tops. Rockfishes were the most frequently observed fishes, especially rosethorn, small sharpchin rockfishes, and large yelloweye (*S. ruberrimus*), and yellowtail rockfishes.

IB-Shallow Cobble Habitat. Three of the transects were at 122–145 m over cobble and lower relief rocks interspersed with soft sediments on the northern portion of the bank (Fig. 1). Rosethorn, yelloweye, canary (*S. pinniger*), and large sharpchin rockfishes occurred near rocks, and zoarcids and longnose skates (*Raja rhina*) were seen in muddier areas.

IIA-Deep Mud-Cobble Habitat. Two of the transects were over mud and cobble substrates in deeper water (185–220 m and 140–148 m, respectively). Rosethorn, greenstriped (*S. elongatus*), canary, and yellowtail rockfishes occurred in these two transects but were absent in deeper transects over mud bottoms. However, the fishes seen on these transects were similar to mud bottom assemblages because of the occurrence of several species of flatfishes. Greenstriped rockfish and Dover sole, *Microstomus pacificus*, occupied soft bottom areas between rocks.

IIB-Deep Mud Habitat. Six transects were over mud, which was the predominant substrate at the deepest depths, 164–300 m, although occasional small rock outcrops or boulders were evident there. Sea urchins, *Allocentrotus fragilis*; sea stars, *Pycnopodia helianthoides*; sea cucumbers, *Parastichopus californicus*; and crabs *Lopholithodes foraminatus* were common in this habitat. All these invertebrates had very patchy distributions. We saw zoarcids, Dover sole, and unidentified flatfishes on all six of these transects, and hagfish (*Eptatretus* sp.); rex sole, *Glyptocephalus zachirus*; slender sole, *Lyopsetta exilis*; sablefish, *Anoplopoma fimbria*; poachers (Agonidae); and skates (Rajidae) on most transects. The deep mud habitat included some species also seen over shallow rock and cobble as well as species only observed over deep mud and cobble (Table 2).

The two cobble subgroups (IB and IIA) are probably transitional habitats between shallow rock (IA) and deep mud (IIB). As such they allow comparisons of the occurrence of fishes on similar bottom types at different depths. Yelloweye and canary rockfish appeared to be more common at shallow than deep cobble, whereas splitnose and greenstriped rockfish, cottids, Dover sole, and other flatfishes were more frequently seen over deep than over shallow cobble. Rosethorn rockfish were common in both subgroups (Table 2).

Six to 22 different species of nonschooling fishes were identified on individual transects. Interestingly, the fewest species of fishes (6–12) were seen on the shallowest dives, over rocky and cobble bottoms (67–149 m; Habitat I), while the greatest number (10–22) were seen on deeper dives over mud and cobble bottoms (164–299 m; Habitat II) (Table 2; Mann-Whitney U–test, $P < 0.01$). This difference would be reduced if the unidentified schooling rockfishes seen in shallow water (see below) could have been included. Average density of nonschooling fishes observed varied greatly (0.02–1.3/m^2) within and among habitat types. No difference was found in the densities between Habitat I and Habitat II (Mann-Whitney U-test, $P > 0.2$). Fish density was highest on dives over slabs of flat rock at 149 m (15A) where large numbers of juvenile rockfishes were seen.

Rockfishes

Because rockfishes were the most numerous and diverse family of fishes seen on our dives (Tables 1, 2) and because they are taxonomically a cohesive group with distinct behavioral patterns, they merit special consideration. Most individuals could be categorized into one of four distinct size groups and behavior patterns: 1) schools of small or juvenile fishes, 2) solitary benthic fishes of intermediate size, 3) pelagic schools of large fishes, and 4) large solitary rockfish near the bottom.

Small Schooling Rockfishes

We saw 24 schools, comprised of 10 to several thousand small (<10 cm) unidentified reddish juvenile rockfishes, during 5 of the 16 dives.

TABLE 2.—Number of nonschooling fishes observed on 21 transects on Heceta Bank, groupings and Table 1 for scientific names. (Because transect lengths

	I: Shallow rock and cobble												
Habitat:	IA: Rock										IB: Cobble		
Depth (m):	67-85	67-85	67-85	72-76	72-76	72-76	104-107	104-107	149	149	145	122-145	122-145
Species / Drive-transect:	2A	2B	2C	9A	9B	9C	12A	12B	15A	15B	11B	11C	11A
Rosethorn RF	25	5	2	37	16	44	24	31	31	12	37	12	28
Yelloweye RF	6				1	3			1		5	3	3
Lingcod	5			1	1	4	1					1	
Small RF	3	2		7		11	12	3	825	30	1	1	
Pigmey RF									126				
Ratfish	2						4						
Sanddab	1												
Cottidae		12	6	3			4	10			1		
Greenstriped RF		3	8				15	4		2			1
Zoarcidae		2	1	19	1		1				2	5	4
Canary RF		2		2					1		3	2	7
Yellowtail RF		2		2	5	5							
Kelp greenling	8	2		1	6	3					1	1	
Wolf-eel		1											
Large RF						2	1	2	4	3	21	5	
Longnose skate						1			1		1	1	1
Sharpchin RF							3	2	751	85	4	6	9
Hagfish							3	4	3				1
Dover sole			1				7	3	1	2			
Redbanded RF									1				
Darkblotched RF				7								4	
Splitnose RF				1							3		
Tiger RF				1								1	
Big skate			1										2
Bathymasteridae								8					
Blenniidae							8						
Stripetail RF											1		
Agonidae												1	
Rajidae													3
Rex sole													1
Flatfish													
Thornyhead													
Arrowtooth Fl													
English sole													
Slender sole													
Pacific hake													
Sablefish													
Ragfish													
Sand sole													
No. fish types	7	9	6	11	6	8	12	9	11	6	12	13	11
No. fish/100 m^2	3.0	4.4	2.2	4.8	3.4	3.6	4.6	6.2	130	14	9.5	5.6	1.5

These schools frequently occurred at the shallowest depths (<85 m) over rugged, rocky topography. Including transects where no schools were seen, the median and mean numbers, respectively, of small schooling rockfishes observed were 750 and 831 at depths <85 m, and 0 and 9.4 at depths >85 m. These schools, usually encountered about a meter off the bottom, often dove toward the bottom when alarmed by the submersible, with individuals dispersing into crevices, rubble, or among the stalks of large anemones.

23-31 August 1987. See Figure 3 for cluster analysis of habitat varied, we compared relative abundances among dives.)

	II: Deep mud and cobble							
Habitat:	IIA: Cobble		IIB: Mud					
Depth (m):	185-220	140-148	244	244	164-222	164-222	290-299	290-299
Species / Drive-transect:	3C	14	5A	5B	6B	6A	8A	8B
Rosethorn RF	27	21						
Yelloweye RF	1					1		
Lingcod			1					
Small RF		3	1		2			
Pigmey RF								
Ratfish			1			1	1	3
Sanddab								
Cottidae	16	17	5				3	
Greenstriped RF	1	21						
Zoarcidae	9	14	14	20	53	8	4	6
Canary RF		1						1
Yellowtail RF	2							
Kelp greenling								
Wolf-eel								
Large RF	5	4			2			
Longnose skate		2			1			1
Sharpchin RF	9		9		1	8	1	
Hagfish			1	1	1	14	7	5
Dover sole	11	29	8	3	10	4	6	12
Redbanded RF	1	1	4					
Darkblotched RF	1							
Splitnose RF		21	1	6				
Tiger RF								
Big skate			1					
Bathymasteridae								
Blenniidae								
Stripetail RF								
Agonidae	1	1	6	51	4	2	1	
Rajidae			1	1		1	1	3
Rex sole	4	2	8	9	4			2
Flatfish	10	3	8	13	2	5	1	1
Thornyhead	1		22				6	4
Arrowtooth Fl	1		1		4			
English sole		4				1	2	
Slender sole		2	2	13	16	65		1
Pacific hake			4					
Sablefish			4	1	2	1	65	67
Ragfish			1					
Sand sole			1					
No. fish types	16	16	22	10	13	12	12	12
No. fish/100 m^2	1.0	6.8	58	5.2	2.6	4.4	7.3	5.5

Solitary Benthic Rockfishes

We saw solitary benthic rockfishes on all dives. The rosethorn rockfish (10–15 cm in length) was the most ubiquitous of all fishes observed on our dives. They were seen on all dives between 67 and 305 m, except the two dives over mud bottom, and ranked first in abundance on 10 of 21 transects (Table 2). They usually occurred singly, resting on soft sediments near rocks, on flat rocks, and occasionally in the depressions of vase sponges. Shortspine thornyheads, *Sebasto-*

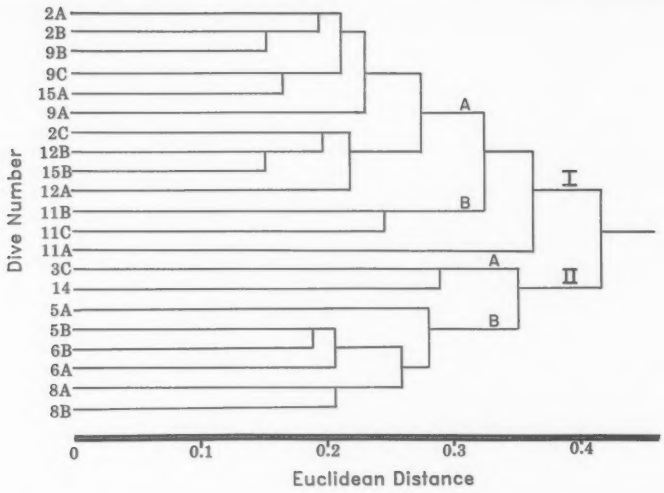

FIGURE 3.—Dendogram showing results of cluster analysis based on presence/absence of fish species from 21 transects. Dive numbers are shown along Y-axis and Euclidian distance along the X-axis. Roman numerals indicate the two major habitat groups and letters indicate subgroups (see Table 2).

lobus alascanus, and greenstriped rockfishes were usually in deep water on mud bottoms and in shallow water on mud or rocky bottoms, respectively (Tables 2, 3). Often thornyheads rested in shallow depressions in the bottom.

Largest concentrations of small- and intermediate-sized benthic rockfishes were seen during a dive at 149 m over rock (15A). Most of these were tentatively identified as sharpchin and pygmy, *S. wilsoni*, rockfishes. Their mean density on this transect was about 1.3/m^2 (Table 2). Pygmy; sharpchin; and Puget Sound, *S. emphaeus*, rockfishes were collected on this dive (Table 3). On another dive (not shown in Table 2), the densities of these small benthic rockfishes in areas of flat rocks, ledges, and cobble were as high as 5–10/m^2 at depths of 120–140 m. These fishes rested among rocks and ledges on the bottom but also swam one or two meters off the bottom. When frightened they often retreated into crevices and under rocks.

TABLE 3.—List of fishes (standard lengths in mm) collected with the slurp gun during five Mermaid dives onto Heceta Bank in August 1987.

Dive 3	
Slender sole	*Lyopsetta exilis* (186, 129)
Smootheye poacher	*Xeneretmus leiops* (170)
Dive 4	
Splitnose rockfish	*Sebastes diploproa* (181)
Bigeye starsnout poacher	*Bathyagonus pentacantha* (186)
Dive 6	
Rosethorn rockfish	*Sebastes helvomaculatus* (162)
Sharpchin rockfish	*Sebastes zacentrus* (132)
Dive 8	
Blacktail snailfish	*Careproctus melanurus* (227)
Dive 15	
Threadfin sculpin	*Icelinus filamentosus* (162)
Spotted cusk-eel	*Chilara taylori* (263)
Thornback sculpin	*Paricelinus hopliticus* (156)
Pygmy rockfish	*Sebastes wilsoni* (179, 148, 141, 136, 129, 117)
Sharpchin rockfish	*Sebastes zacentrus* (132, 92, 82)
Puget Sound rockfish	*Sebastes emphaeus* (101)

Large Schooling Rockfishes

Schools of large (30–50 cm) rockfishes were seen on five of the dives where bottom depths were less than 150 m. No schools of large rockfishes were seen in deeper water. These shallow-water schools were predominantly of yellowtail rockfish and occasionally of canary rockfishes. Other than an occasional canary or

[2]These fish had two white stripes, one above and one below the lateral line, with reddish pigmentation over the rest of the body.

yellowtail rockfish in a school of similar-sized yellowtail rockfish, all schools were comprised of fish of one species, all about the same size. Observers in the submersible sometimes located schools where echo-groups, probably caused by aggregations of large schooling rockfishes, were recorded by the surface vessel's echosounder. The sound scatterers were often prominent as spires close to topographic pinnacles or elevated rocky outcrops.

Yellowtail rockfish schools were attracted to and followed the submersible on several dives. On one dive, a school of 500–1000 fish stayed near the submersible for over an hour. The school either followed the submersible, or circled when it stopped, before abruptly turning away. Individual fish were usually 3–4 body lengths apart and could be clearly seen with ambient light at a depth of about 100 m. When the submersible lights were turned on, fish sometimes "flinched" but did not swim away. On another dive, a school of several hundred yellowtail rockfish were encountered while the submersible descended; they remained in view most of the way to the bottom. At first they actively swam downward, but at 100 m they passively sank, oriented head-down. When the thrusters were turned on, this school disappeared, but once the submersible was on the bottom, the school approached and swam around the submersible.

Large Near-Bottom Rockfishes

The best example of this category is the yelloweye rockfish. Large individuals of this species were seen in shallow water swimming above rock or cobble. Canary and yellowtail rockfishes, though more pelagic, sometimes were seen singly near the bottom. Although large rockfish usually were not resting on the bottom, yellowtail, splitnose (*S. diploproa* >30 cm), yelloweye, greenspotted (*S. chlorostictus*), and tiger (*S. nigrocinctus*) were observed doing so occasionally.

Rockfish Coloration. Splitnose rockfish sometimes changed color dramatically during and after collection. In situ, most individuals had strikingly red and white vertical bars extending almost to the ventral surface, but one that was chased blanched to almost all white. Another (181 mm SL) that was captured had lost its prominent white bars at the surface, appearing a dull red overall as shown in Eschmeyer et al. (1983). Straty (1987) also noted dramatic changes in the coloration of juvenile rockfishes in sita and after they were examined at the surface.

The yellowtail rockfish we observed had 3–5 very vivid large white spots above the lateral line. These spots faded to indistinct pale spots on live yellowtail brought to the surface by hook and line. The white spots on rosethorn rockfish were also less prominent on fish captured and brought to the surface than on those seen in situ.

Fishes Collected

In addition to several large benthic invertebrates, we collected 21 individuals and 12 species of fishes using the slurp gun (Table 3). Six species of rockfishes were also captured using hook and line from the support vessel: yellowtail, canary, yelloweye, rosethorn, greenspotted, and the bank (*S. rufus*) rockfishes. The last fish was not identified from the submersible. The liparidid *Careproctus melanurus* was also seen on several dives (but not during transects) and was collected by slurp gun.

DISCUSSION

The diverse physical habitats encountered during our dives correlated with differences in the species composition and abundances of fishes. Two species groups were identified: one primarily comprised of rockfishes in shallow water on rock and cobble, and one that included zoarcids, several species of flatfishes, agonids, and sablefish in deep water mostly over soft substrates. Greenstriped and splitnose rockfishes and shortspine thornyheads were most common over soft substrates, whereas most other scorpaenids were seen most frequently in rocky habitats in shallow water. Richards (1986) also noted that greenstriped rockfish were most abundant over fine-sediment habitats in the Strait of Georgia, British Columbia, whereas yelloweye rockfish preferred rock wall and more complex habitats at shallower depths.

Most species were broadly distributed (Table 2). There was much overlap in species distributions, and species associations were indistinct. Habitat type and depth varied together, however, with rock habitat occurring predominantly in shallow water and mud in deep water. Although cobble habitats were identified at two depths, these data were inadequate for examining bathymetric segregation of rockfish species within habitat types, as has been documented for

certain shallow-water species (Larson 1980; Hallacher and Roberts 1985).

Heceta Bank, and probably other rocky banks off the Pacific Northwest and Southeast Alaska, appear to be important juvenile nursery areas for rockfishes. Dense schools of pelagic juveniles and adult yellowtail rockfishes were observed only over the rocky, high-relief areas on the top of the bank, and high densities of benthic juveniles were found only on the flanks of the bank and not in deeper waters of the bank (Table 2). Straty (1987) and Carlson and Straty (1981) observed large schools of young rockfish near rocky pinnacles and boulder fields at depths <171 m off southeastern Alaska, and concluded that these areas were nursery grounds for rockfish. They collected specimens of Pacific ocean perch, *S. alutus*; sharpchin, pygmy, and Puget Sound rockfishes; and shortspine thornyheads on the bottom, species (with the exception of *S. alutus*) that we captured on Heceta Bank (Table 3).

Some of our submersible dives were close to locations previously sampled by trawl surveys of the Oregon Department of Fish and Wildlife (ODFW) (Barss et al. 1982). In the ODFW surveys, commercial trawls designed for catching rockfishes on rough terrain (Atlantic Western and Box Mystic trawls) were used with roller gear to keep the footrope off the bottom. The cod end of these nets was usually made of 11.4 cm mesh. During 1980–81, a total of 27 tows were made between 132 and 210 m, within about 4 km of Dive Site 11 (145 m) (Fig. 2).

Fish assemblages in trawl catches and in submersible observations from adjacent areas differed. Only 8 of the 25 trawl-caught species were seen from the submersible on Dive 11, and 7 of the species observed during the dive were not caught in trawls (Table 4). Five species of rockfishes, however, were among the most numerous 11 species by both methods. *Sebastes pinniger* dominated trawl catches by number and weight (comprising 88% of the total weight of the catches), but it was not seen many times from the submersible.

TABLE 4.—Composition of fishes by percentage calculated from numbers during submersible dives and caught in trawls from the same general area near Heceta Bank. The weight of individual species caught in trawl catches were converted to numbers of a species by dividing by the average weight of individuals.

Dive 11		Bottom trawl	
%	Species	%	Species
30.1	Schooling *Sebastes* spp.	76.2	*Sebaster pinniger*
29.4	*Sebastes helvomaculatus*	10.1	*Sebastes zacentrus*
10.7	*Sebastes* unidentified	2.5	*Sebastes flavidus*
7.2	*Sebastes zacentrus*	2.1	*Sebastes helvomaculatus*
4.6	*Sebastes pinniger*	1.5	*Merluccius productus*
4.2	*Sebastes ruberrimus*	1.2	*Ophiodon elongatus*
4.2	Zoarcidae	1.2	*Sebastes jordani*
1.5	*Sebastes crameri*	1.0	*Sebastes elongatus*
1.1	Rajidae	1.0	*Sebastes proriger*
1.1	*Sebastes diploproa*	0.6	*Sebastes brevispinnis*
1.1	*Raja rhina*	0.4	*Squalus acanthias*
0.8	*Hexagrammos decagrammus*	0.4	*Anoplopoma fimbria*
0.8	*Raja binoculata*	0.4	*Trachurus symmetricus*
0.4	*Sebastes elongatus*	0.3	*Hydrolagus colliei*
0.4	*Ophiodon elongatus*	0.2	*Sebastes ruberrimus*
0.4	Cottidae	0.2	*Sebastes paucispinis*
0.4	*Sebastes nigrocinctus*	0.2	*Microstopmus pacificus*
0.4	*Sebastes saxicola*	0.1	*Hippoglossus stenolepis*
0.4	*Eptatretus stouti*	0.1	*Parophrys vetulus*
0.4	Agonidae	0.1	*Glyptocephalus zachirus*
0.4	*Glyptocephalus zachirus*	0.1	*Sebastes entomelas*
		<0.1	*Oncorhynchus tshawytscha*
		<0.1	*Eopsetta jordani*
		<0.1	*Raja rhina*
		<0.1	*Atheresthes stomias*

Both of the assessment methods have biases, and differences between them are to be expected. The trawls were designed to avoid contact with the bottom and sampled a large volume of water at a greater distance above the seafloor and retained mostly large fishes, whereas the submersible was most effective for surveying small fishes on or close to the seafloor. Most large pelagic fishes probably avoided the submersible. Although yellowtail rockfish were attracted to the submersible, only a small fraction of the individuals in schools were visible from the viewing port. Differences in sampling locations and times undoubtedly contributed to differences in species composition. Thus quantitative surveys from submersibles appear to be most useful for assessing fishes closely associated with the sea floor, for comparing relative abundances among habitats, and for studying fine-scale distributions of fishes.

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NOTES

Comparative Standing Stocks of Mesozooplankton and Macrozooplankton in the Southern Sector of the California Current System

The long-term (40-year) time series of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has characterized low frequency changes in ocean circulation, macrozooplankton biomass, and ichthyoplankton and holozooplankton populations (Reid et al. 1958; Brinton 1981; Chelton et al. 1982; Smith 1985; McGowan 1985; Roesler and Chelton 1987). The Atlas series of the CalCOFI program provides extensive summaries of the hydrography of the California Current system and the large-scale distribution of its planktonic fauna (Atlas Nos. 1–30, Scripps Institution of Oceanography 1963–82). These investigations constitute an excellent foundation for studies ranging from experimental work with individual pelagic species to projections of global climate effects on ocean populations and production.

The primary emphasis of the zooplankton component of the CalCOFI program has been the larger macrozooplankton (>505 μm) and the ichthyoplankton. In the present study, we assess the biomass of the mesozooplankton (defined here as the zooplankton fraction passing through a 505 μm mesh net but retained in a 202 μm mesh net) in comparison with that of the historically sampled macrozooplankton. Efforts to close budgets of material and energy in the California Current system (Roemmich 1989) may require consideration of the contributions of the mesozooplankton to standing stocks and metabolic transformations. Further, given the selective nature of predation by planktivorous fish in this region (Arthur 1976; Koslow 1981), the mesozooplankton may be disproportionately significant as prey items to particular size classes of pelagic predators.

Materials and Methods

Comparisons of mesozooplankton and macrozooplankton standing stock were carried out between September 1986 and May 1987. A *ver*tically *r*etrieved *b*ongo (VERB) net frame was used to take paired zooplankton samples (Fig. 1). The net incorporated features of the Brown and Honegger (1978) vertical net and the McGowan and Brown (1966) oblique bongo net, with several differences. Unlike the Brown and Honegger net, the net rings did not hinge and presented less surface area. In contrast to the bongo net, the VERB frame did not pivot around a central axis, and the system was designed to filter only during vertical ascent rather than during oblique descent and ascent. The net mouth

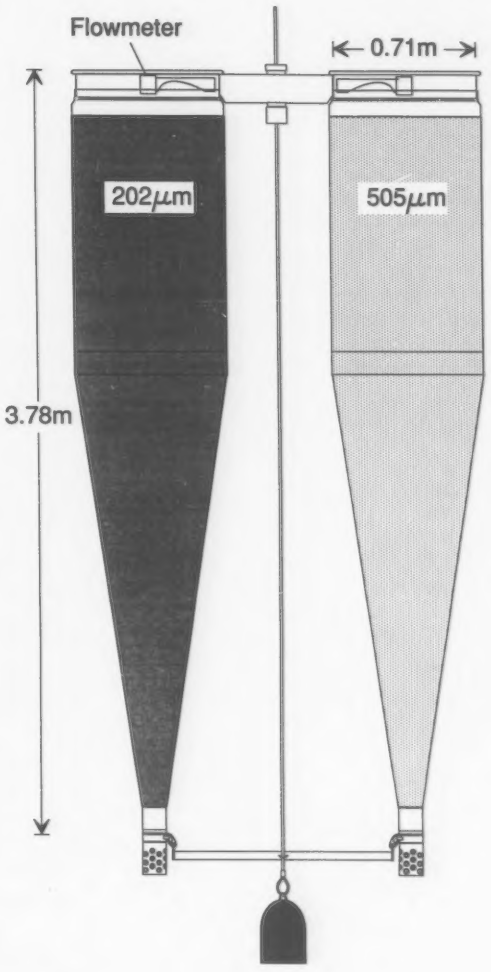

FIGURE 1.—Illustration of VERB frame and nets.

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openings were each 71 cm in diameter and the net open area ratio was no less than 5.0 (Tranter and Smith 1968). A 100 kg weight was secured to the end of the hydrowire. TSK flowmeters[1], modified to display flow counts digitally, were mounted inside both net rings. The frame was deployed with one 202 μm Nitex mesh and one 505 μm mesh net, each with rigid cod ends having apertures of the same mesh size.

The VERB frame was lowered at a speed of 40–50 m min^{-1} to 200 m and retrieved at 60 m min^{-1}. Each net filtered approximately 80 m^3 of water, minimizing clogging of the finer mesh net. Rapid deployment and recovery, combined with maneuvering the research vessel, served to minimize deviation of the hydrowire angle from the vertical. Wire angles were recorded at least four times during ascent.

Preliminary VERB net trials were carried out on cruise Verb1 (11–12 September 1986; see Figure 2). VERB deployments were then made on four CalCOFI cruises, designated 8609 (21–29 September 1986; N = 28 stations), 8611 (15–24 November 1986; N = 26), 8703 (5–14 March 1987; N = 27), and 8705 (3–12 May 1987; N = 30). The primary stations sampled were along two lines orthogonal to the coastline (lines 80 and 90); additional stations occupied the nearshore segment of lines 83 and 87 (Fig. 2). Time constraints precluded taking VERB samples at all CalCOFI stations.

Zooplankton samples were preserved in 10% formalin buffered with sodium borate. In the laboratory, the sample obtained with the 202 μm net was washed through a 505 μm mesh nested inside a 75 μm mesh, yielding a fraction between 202 μm and 505 μm ("mesozooplankton") and one greater than 505 μm ("macrozooplankton"). The sum of these two fractions is referred to as "total" net zooplankton, although it quite clearly omits the microzooplankton that are certain to be of considerable significance (Beers et al. 1980; Fenchel 1988). Biomass of zooplankton samples was determined first by measuring displacement volume (Ahlstrom and Thrailkill 1963), then by

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

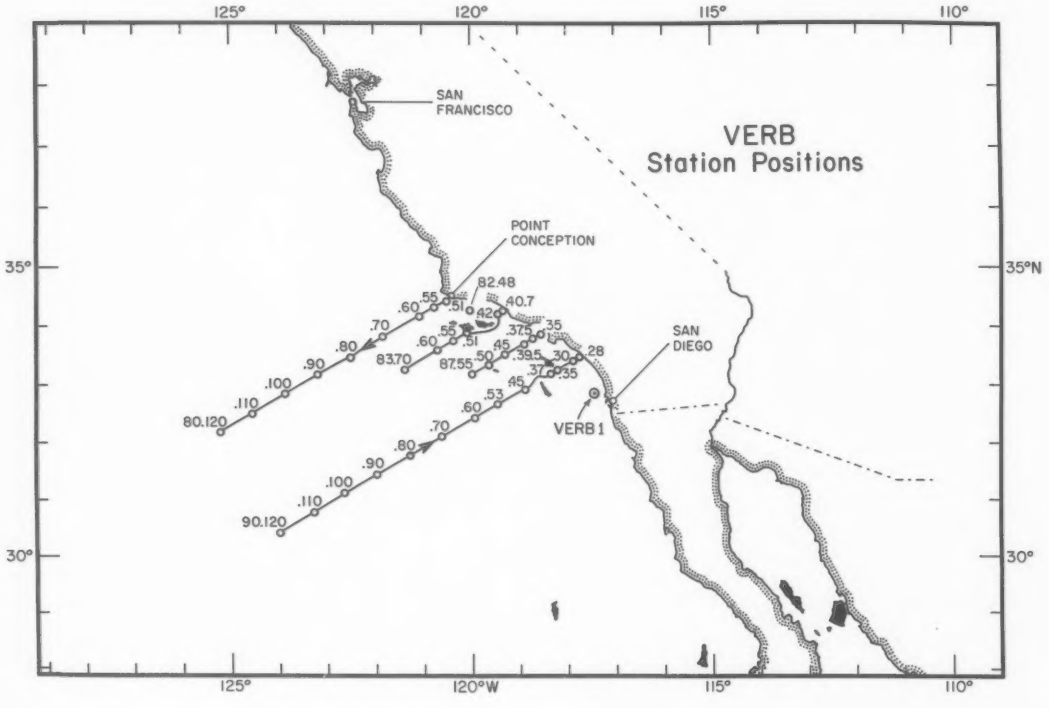

FIGURE 2.—Stations occupied in the southern sector of the California Current. Position of cruise VERB1 is noted, as well as the VERB zooplankton stations sampled on 4 CalCOFI cruises. Note that all indicated stations could not be sampled on every cruise.

measuring ash-free dry mass on a ¼ split of the sample obtained with a Folsom splitter. A split was filtered onto a pre-ashed Whatman GF/C filter, rinsed with a solution of 6% aqueous ammonium formate, and dried at 60°C. After weighing, the sample was ashed in a muffle furnace at 500°C for 4 hours then reweighed to determine ash-free dry mass by difference.

Standing stocks were expressed per unit volume, using the volume filtered by each net as determined from calibrated flow meters.

Water bottle samples for chlorophyll a (Chla) analyses were typically taken at 12–14 depths in the upper 200 m of the water column. Following filtration onto GF/C glass fiber filters, pigments were extracted in refrigerated 90% acetone in the dark and analyzed fluorometrically (Venrick and Hayward 1984). Chla between the surface and 150 m was integrated vertically using the trapezoidal rule. A complete report of chlorophyll data and detailed sampling information may be found in SIO References 87-7 and 87-19 (Scripps Institution of Oceanography 1987a, b).

RESULTS

Several characteristics of the VERB system were analyzed to determine its sampling bias, precision, and estimated filtration efficiency.

Right/Left Bias: A series of replicated vertical hauls was carried out with 202 μm nets mounted on both sides of the VERB frame. This was done over a 2½–3 h interval on 2 occasions. No bias was detected between the ash-free dry mass (AFDM) retained by the left and right nets on either 11 September (N = 9 hauls, $P > 0.10$, Wilcoxon Signed Rank test) or on 26 September (N = 8 hauls, $P > 0.10$).

Precision: Precision of replicated 202 μm vertical hauls, expressed as the coefficient of variation (100 × SD/$\bar{x}$), was determined on 3 occasions, again over 2½–3 hours. Coefficients of variation of AFDM on 3 trials were 18.2% (N = 18 samples, 9 hauls), 14.1% (N = 16 samples, 8 hauls), and 17.0% (N = 13 samples, 13 hauls).

Filtration Efficiency: Filtration efficiency of the 202 μm VERB net was compared against that of the 505 μm VERB net using the respective volumes of water filtered. Filtration efficiency of the 202 μm net averaged 99.4 ± 1.4% ($\bar{x}$ ± 95% C.L., N = 126 comparisons) of that of the 505 μm net, reflecting negligible clogging of the finer mesh net.

Wire Angles: The median wire angle (off the vertical) was 7°. Eighty-six percent of the angles were ≤12° (N = 144). Apart from unusually strong wind conditions when the net could not be deployed, wire angles could generally be maintained at acceptable levels (<10–12°) by maneuvering the vessel.

202 μm vs. 505 μm Nets: Retention characteristics of the 2 nets were compared from the >505 μm fraction displacement volume. The median ratio of the >505 μm displacement volume from the fine:coarse mesh nets was 1.17 (nonparametric 95% C.L.: 1.09–1.24, N = 123). The departure from a ratio of 1.00 probably reflects a difference between retention characteristics of the 505 μm plankton mesh in the field and in the laboratory. Larger organisms apparently show less escapement through 505 μm mesh under low pressure differential in the laboratory, compared with the high pressure differential across the mesh of a net under tow. To avoid introducing a systematic bias, further analyses are therefore restricted to the 2 fractions (<505 μm, >505 μm) collected by the 202 μm net.

Ash Content: The ash content of the 2 size fractions did not differ significantly ($P > 0.05$). Ash content as a percentage of total dry mass averaged 16.0% ± 0.9% ($\bar{x}$ ± 95% C.L., N = 160) for the fraction <505 μm and 14.6% ± 0.7% for the fraction >505 μm.

Standing Stocks: The relation between displacement volume and AFDM appeared relatively linear when expressed on a log-log scale (Fig. 3A). However, closer inspection revealed that the slope of this relation differed for the 2 size fractions (P<0.001, Analysis of Covariance). Hence a joint regression line was inappropriate. When replotted separately on linear axes, the difference in these relations was more apparent (Fig. 3B, C). A rectilinear function provided an adequate least squares fit for the fraction <505 μm (Table 1). However, the relation was nonlinear for the fraction >505 μm. Use of a curvilinear function (Table 1) decreased the residual sum of squares and removed the serial correlation of residuals that was apparent in a straight line fit ($P < 0.05$). For the fraction >505 μm, a linear relation was a particularly poor

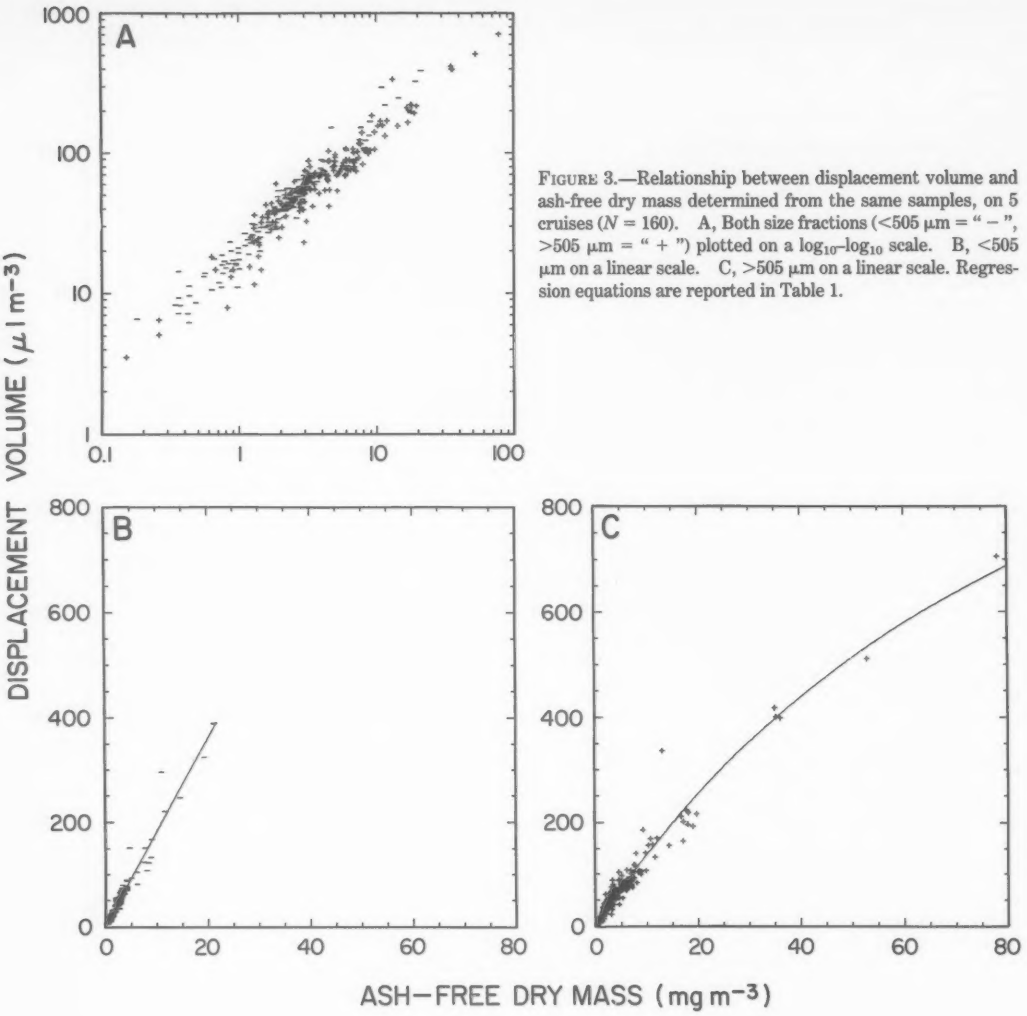

FIGURE 3.—Relationship between displacement volume and ash-free dry mass determined from the same samples, on 5 cruises ($N = 160$). A, Both size fractions (<505 μm = " – ", >505 μm = " + ") plotted on a $\log_{10}$–$\log_{10}$ scale. B, <505 μm on a linear scale. C, >505 μm on a linear scale. Regression equations are reported in Table 1.

descriptor at low AFDM values. The F-statistic was inappropriate for testing the goodness-of-fit of a nonlinear curve (Draper and Smith 1981), but the F-ratio reported in Table 1 provided a relative indicator of the adequacy of the regression equation. The fitted curve in Figure 3C was merely an empirical fit that was not meant to imply any theoretical relation. Because of this nonlinearity, perhaps caused by the compressibility of larger organisms at high biomass levels, AFDM was used for subsequent comparisons.

Since both displacement volume and AFDM have natural variability, a functional regression (Laws and Archie 1981) would be a more appropriate statistical model to apply to the data in Figure 3. However, the need for a nonlinear relationship for the >505 μm fraction complicates the use of a functional regression model. For consistency, the fit for both size fractions is therefore based on predictive regressions with the attendant possibility of introducing biased estimators (Sokal and Rohlf 1981). Users of functional regressions should note that the equation for estimating the confidence interval of the regression slope reported in Jensen (1986; equation 14) is in error.

A comparison of mesozooplankton and macrozooplankton standing stocks for four pooled CalCOFI cruises is illustrated in Figure 4. The median contribution of the mesozooplankton to

TABLE 1—Regression relationships between displacement volume (DV; $\mu L\ m^{-3}$) and ash-free dry mass (AFDM; $mg\ m^{-3}$). *F*-ratio designates the ratio of regression mean square: residuals mean square. Regression *P*-value indicates the significance of a linear regression, and the residuals *P*-value indicates the significance of the first order serial correlation of regression residuals. $N = 160$ for both size fractions.

Size fraction	Equation	*F*-ratio	Regression *P*-value	r^2	Residuals *P*-value
<505 μm	DV = 17.86(AFDM) + 3.86	2,869.1	<0.001	0.938	>0.10
>505 μm	$DV = \frac{1594.7(AFDM)}{105.5 + AFDM}$	2,725.6	—	—	>0.10

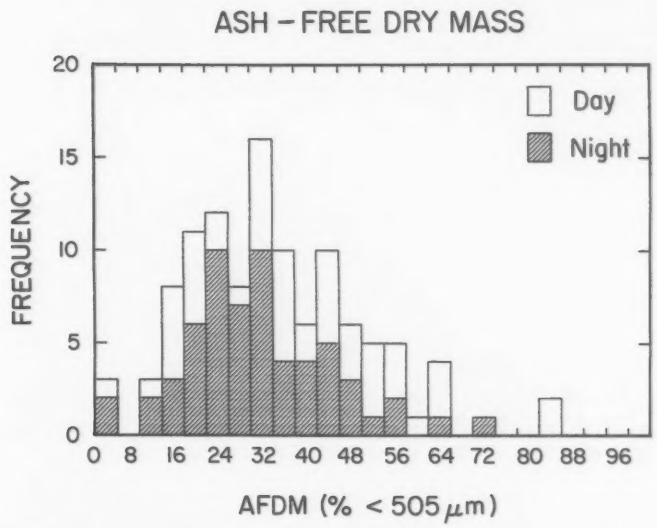

FIGURE 4.—Frequency distribution of the percentage of ash-free dry mass in the fraction <505 μm, from 4 CalCOFI cruises ($N = 111$).

the total standing stock was 30.2%. Partitioned by time of sampling, the day mesozooplankton averaged 35.0% and the night mesozooplankton 28.1% of total standing stock. Day and night medians differed significantly ($P < 0.05$, Mann-Whitney U test). The higher proportion of macrozooplankton (>505 μm) in nighttime samples probably reflects nocturnal vertical migration of larger zooplankton into the upper 200 m of the water column or, perhaps, diurnal net avoidance. At individual stations, the mesozooplankton contribution ranged up to 82% of the total.

Despite considerable variance in the relationship, zooplankton standing stocks were positively correlated with the Chla concentration (Fig. 5). This relation, apparently curvilinear, is illustrated as log AFDM plotted against the log maximum Chla concentration in vertical profile at each station for the fraction <505 μm (Fig. 5A: $r = 0.73$, $P < 0.001$, Spearman's rank correlation, $N = 110$) and that >505 μm (Fig. 5B: $r = 0.70$, $P < 0.001$, $N = 110$). When plotted against the log chlorophyll integrated to 150 m the correlation coefficients were slightly smaller (<505 μm: $r = 0.71$; >505 μm: $r = 0.64$).

The relative contribution of mesozooplankton to total standing stocks varied independently of Chla concentration. Neither in the day samples ($r_s = -0.117$, $P > 0.10$, $N = 49$) nor in the night samples ($r_s = 0.060$, $P > 0.10$, $N = 61$) was the fraction of standing stock <505 μm associated with Chla (Fig. 6).

Sufficient samples to analyze cross-shore gradients in total standing stock and in the percentage of standing stock contributed by the mesozooplankton were obtained only along lines

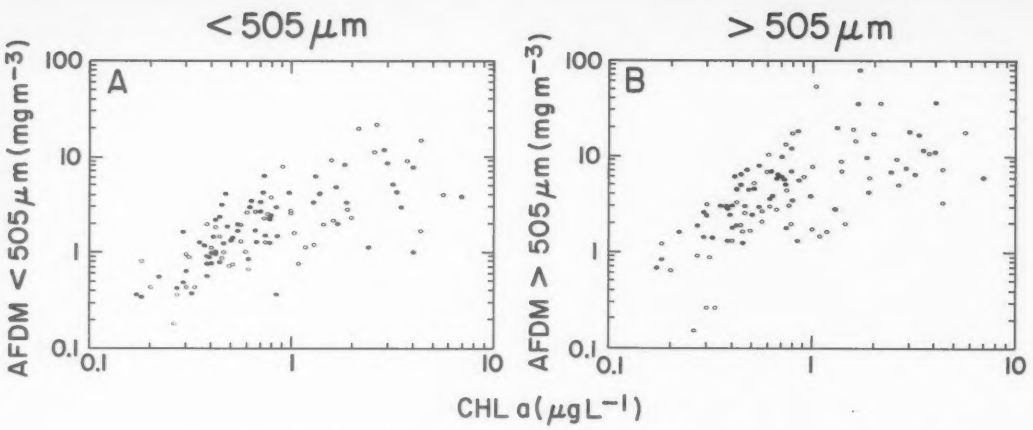

FIGURE 5.—Relationship between ash-free dry mass (AFDM) and maximum Chl*a* concentration, from 4 CalCOFI cruises. Open circles are day samples, closed circles are night samples. A, AFDM <505 μm; B, AFDM >505 μm.

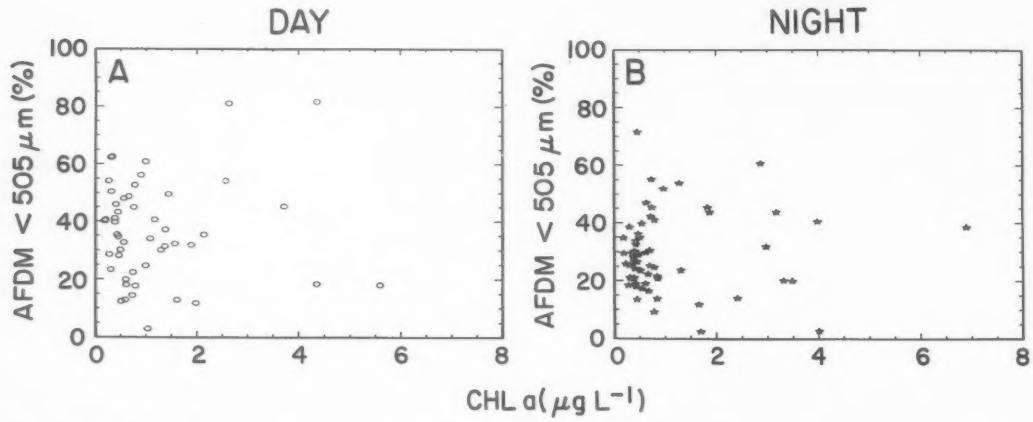

FIGURE 6.—Relationship between the percentage of ash-free dry mass in the fraction <505 μm and Chl*a* concentration, from 4 CalCOFI cruises. A, Day samples; B, night samples.

80 and 90. (Even so, the two offshore stations along line 80 were sampled only on cruise 8609.) Samples from lines 83 and 87 are included in Figures 3–6 but were not analyzed for spatial trends. Along both line 80 and line 90 the 4-cruise average of total AFDM decreased in the cross-shore direction (Fig. 7A, B). On individual cruises a secondary maximum of standing stock often occurred offshore along line 80 (e.g., cruises 8609, 8705) and line 90 (e.g., cruises 8609, 8703, 8705).

The percentage of zooplankton standing stock <505 μm also exhibited some cross-shore trends. On both lines 80 and 90, the median value was highest at the station closest to shore (Fig. 7C, D). On line 80 the median value first decreased then remained relatively constant in the offshore direction. On line 90 the median value decreased to station 80 then appeared to increase again at the more offshore stations. (This apparent offshore increase at stations 110 and 120 may have been influenced by a higher incidence of daytime samples.) That is, mesozooplankton appeared to make a larger contribution to standing stock at the most inshore stations and possibly at the most offshore stations along line 90.

DISCUSSION

These results demonstrate that, on average, approximately one third of the >202 μm zoo-

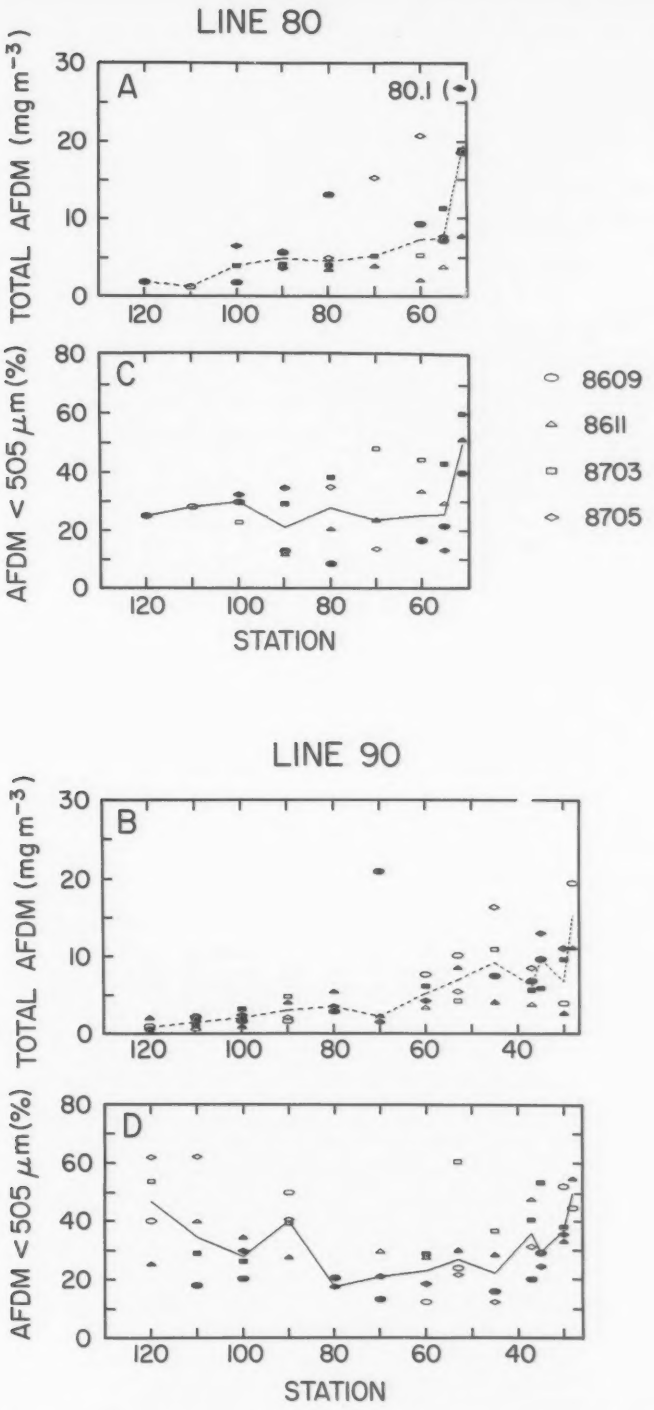

FIGURE 7.—Cross-shore distributions of total ash-free dry mass along (A) line 80 and (B) line 90, and percentage of ash-free dry mass in the fraction <505 μm along (C) line 80 and (D) line 90. Stations along lines 80 and 90 are aligned vertically. Dashed and solid lines illustrate the median values.

plankton standing stock is in the mesozooplankton fraction in this sector of the California Current system. Considerably higher contributions occur in some regions and on some occasions. It is difficult to estimate the contribution of this standing stock to heterotrophic processes such as grazing, oxidative metabolism, and fecal pellet fluxes without further information on the species composition of the two size fractions. However, because physiological processes depend on body mass (Banse and Mosher 1980), the mesozooplankton would contribute disproportionately to these water column processes.

Consider, for example, *Paracalanus parvus*, a relatively small-bodied copepod representative of the mesozooplankton retained by a 202 μm mesh net, and the larger copepod *Calanus pacificus* and euphausiid *Euphausia pacifica*, the latter two representative of the macrozooplankton captured by a 505 μm mesh net. The maximum daily specific ingestion rate of *P. parvus* females is 1.0–2.2 d^{-1} (varying on a carbon and a nitrogen specific basis, Checkley 1980), while that of *Calanus pacificus* is ca. 0.4 d^{-1} (Frost 1972) and that of adult *Euphausia pacifica* is ca. 0.08 d^{-1} (Ohman 1984). Based on these mass-specific rates, if 30.2% of the zooplankton standing stock were *P. parvus*-like organisms and the remainder were evenly split between *Calanus*-like and *Euphausia*-like organisms, the mesozooplankton could account for 79% of the grazing pressure. The presence of larvaceans and salps would alter this estimate because these gelatinous organisms are relatively large but have higher specific rates of metabolism than most crustacean zooplankton (Alldredge and Madin 1982). Furthermore, the estimate ignores the presence of omnivores and predators and assumes, unrealistically, food-satiated ingestion rates for all taxa. Nevertheless, the mesozooplankton is doubtless a significant contributor to heterotrophic processes.

The increased contribution of the mesozooplankton in the most inshore domain may reflect the presence of early developmental stages of zooplankton species that show relatively high rates of reproduction inshore (Brinton 1976; Checkley 1980; Smith et al. 1986). The possible trend toward a larger contribution of mesozooplankton offshore along line 90 requires corroboration. Much further to the west, in the oligotrophic central North Pacific, 20–40% of the zooplankton standing stock collected with a 183 μm net was <500 μm (Rodriguez and Mullin 1986).

The relation between displacement volume and ash-free dry mass for both size fractions combined is qualitatively similar to that reported in Wiebe et al. (1975, fig. 4a); however, their regression includes several size categories and their dry mass values apparently included ash, so that the two studies are not strictly comparable.

Whether the relative importance of mesozooplankton varies through time, such as during El Niño-Southern Oscillation (ENSO) conditions, is unknown. Smith (1985) documented an appreciable compositional change within the macrozooplankton during the strong ENSO of 1957–59. For example, comparing 1956 and 1958, the average thaliacean (primarily salp, larvacean, doliolid) biomass decreased 27-fold while the total copepod biomass decreased by only ½ during this ENSO (Smith 1985), suggesting differential responses to ENSO events by different members of the pelagic food web.

How such compositional changes within the macrozooplankton might relate to changes in the relative importance of mesozooplankton organisms is not obvious. Since phytoplankton concentrations can decrease markedly during ENSO conditions (Fiedler 1984), the argument could be made that smaller zooplankton, which generally have lower food requirements to sustain growth and reproduction (Huntley and Boyd 1984), might increase in relative abundance. However, the lack of correlation between the fraction of zooplankton <505 μm and Chla suggests that chlorophyll alone is too simple a measure of food availability. Microzooplankton may also be an important prey source. And it should be noted that a model based on energetic considerations makes a contradictory prediction, namely increased body size in oligotrophic regions (Gerritsen and Kou 1985). Additional information beyond food requirements must also be considered, including life history traits and species composition of the constituent zooplankton, as well as mesoscale circulation effects on species distributions (Haury et al. 1986).

The present evidence for the significance of the mesozooplankton in the California Current system is based upon a bulk measure of zooplankton standing stock. Future efforts directed toward understanding the mechanisms of response of planktonic organisms to environmental change should take account of species-specific responses of the mesozooplankton.

ACKNOWLEDGMENTS

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Tuna Larvae Abundance: Comparative Estimates from Concurrent Japanese and Australian Sampling Programs

When estimating the absolute abundance of organisms, the accuracy and bias of sampling methods should be assessed (Andrew and Mapstone 1987). In ichthyoplankton sampling the absolute abundance of organisms will probably never be known; the characteristics of accuracy and bias in different sampling methods can only be inferred by concomitant sampling of the same population. The Fishery Agency of Japan Far Seas Fisheries Research Laboratory (FSFRL) has used a 2 m ring net to sample ichthyoplankton for many years. It has been the principal tool for sampling tuna larvae, particularly southern bluefin tuna, in the eastern Indian Ocean (Yabe et al. 1966; Ueyanagi 1969; Yonemori and Morita 1978; Yukinawa and Miyabe 1984; Yukinawa and Koido 1985). The net routinely samples large volumes of water (approximately 5,000 m^3 in a 30-min oblique tow), yet catches of tuna larvae on these surveys are generally low. These low catches may reflect a naturally low abundance of tuna larvae, a contention supported by previous studies (Wade 1951; Strasburg 1960; Klawe 1963; Richards 1969; Richards and Simmons 1971; Conand and Richards 1982). In this paper we compare catches of tuna larvae by traditional Japanese methods with those developed by CSIRO Division of Fisheries for quantitative surveys. A series of simultaneous tows were made by the CSIRO, FRV *Soela* and the FSFRL, FRV *Shoyo Maru* on the southern bluefin tuna spawning grounds in the east Indian Ocean in January 1987.

Methods

Two identical 2 m ring nets were deployed concurrently by the FSFRL (Fig. 1, Table 1) in surface and oblique tows. For the oblique tow, a predetermined length of warp (approximately 130 m) was rapidly paid out from the stern so that the net reached a depth of 30 m (approximately 4–10 minutes). The warp was then retrieved at a fixed rate until the net reached the surface (approximately 21–26 minutes). The tow profile actually achieved was determined after the tow from traces made by the depth distance recorder. The 20-min surface tow was deployed close to the hull on the starboard side, amidships, with approximately 7/8 of the net below the surface, fishing a depth range of 0–1.75 m.

Two identical 70 cm ring nets were deployed concurrently by CSIRO (Fig. 1, Table 1) in surface and oblique tows. The oblique tow fished from the surface to the thermocline (the thermocline during the experiment was at approximately 32 m) to cover the full known depth range of the tuna larvae (CSIRO, unpubl. data). An operator, guided by real-time depth information from a sensor on the net, produced a V-shaped tow profile, with a descent time of approximately 8 minutes and an ascent of 12 minutes. The surface tow was deployed for 10 minutes, concurrent with the oblique tow, from a boom on the port side amidships, clear of the wake of the vessel. It was towed approximately 0.5 m under the surface, oscillating between about 0 and 2 m due to the roll of the vessel in the 0.5 m swell.

The volume of water filtered for each net was calculated in the following ways. The volumes filtered by both surface and oblique tows with the 70 cm net were calculated from the distance travelled, measured by calibrated flowmeter readings inside the net, and the mouth area of the net. Volumes filtered by oblique tows with the 2 m net were calculated from the distance travelled (determined from the depth distance recorder behind the net) and the mouth area of

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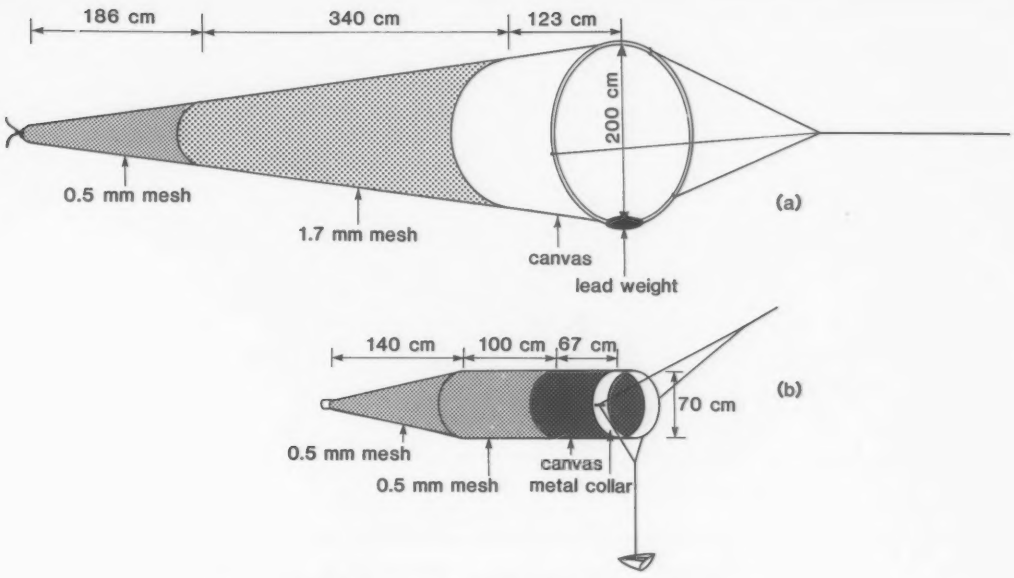

FIGURE 1.—The 2 m and 70 cm nets in their deployed configuration.

TABLE 1.—Specifications of the 70 cm net used by CSIRO and the 2 m net used by FSFRL.

Specification	70 cm net	2 m net
Shape	cylindrical-conical	conical
Mouth opening	70 cm internal diameter, circular, maintained by aluminium collar 18 cm wide	200 cm internal diameter, circular, maintained by galvanized iron pipe
Mouth area	0.385 m^2	3.142 m^2
Net material	Estal monofilament, plain with mesh aperture of 0.5 mm throughout	forward section of multifilament, twist lock with mesh aperture of 1.7 mm, followed by nylon monofilament, plain with mesh aperture of 0.5 mm
Net colour	dyed dark blue	natural (white)
Canvas collar	67 cm width	123 cm width
Bridle	two-wire	three-rope
Depressor	22 kg Scripps attached by two-wire bridle	30 kg weight attached to frame
Flowmeter	General Oceanics[1] mechanical, attached inside mouth frame 17 cm from rim	Tsurumi-Seiki depth distance recorder, towed behind the net
Cod end	solid, thread mounted PVC with 0.5 mm stainless steel drainage screen	netting tied at end to form soft cod end

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

the net. The 2 m net used at the surface was not fitted with a meter so the distance travelled was estimated from the ships speed (2 knots) and the tow duration (20 minutes). Only the submerged mouth area of the 2 m net was used to calculate the volume filtered.

The *Soela* and the *Shoyo Maru* met on 27 January 1987 at lat. 15°S, long. 116°E. The two

vessels, approximately 250 m apart, steamed at 2 knots. Concurrent surface and oblique tows were made by both vessels at six stations in daylight between 1300 and 1700 h local time; the start of tows on each vessel was co-ordinated by radio and visual communication. The distance separating the two vessels during the tows was determined by radar.

The plankton samples taken by the 70 cm net were preserved in 95% ethanol and those from the 2 m net in 10% formalin. Samples were sorted, and tuna larvae identified to species (where possible) and measured (standard length) in the respective laboratories. At FSFRL the samples were sorted in petri dishes with the unaided eye, whereas at CSIRO samples were sorted in a rotatable sorting ring under a dissecting microscope with dark-field illumination. Both laboratories used a dissecting microscope to aid in identification of larvae.

The relative efficiency of the 70 cm and 2 m nets was described by ratios of the mean catch per unit volume for each method of deployment (surface and oblique tows) assuming that small catches are more prone to error than large catches (Snedecor and Cochran 1967). The significance of differences in the number of tuna larvae per unit volume collected by the 2 m and 70 cm net in surface and oblique tows was tested by two-factor ANOVA of split-plot design (Winer 1971). The data were log $(x + 1)$ transformed to make variances homogeneous (Cochran's test; $C = 0.47$; df = 4,5; $P > 0.05$). Differences in the mean lengths of larvae caught by net type and tow type were analyzed by the Kruskal-Wallis test (corrected for ties), and multiple comparisons (with unequal sample sizes) were made using the Dunn test (Zar 1984).

Results

The stations were at approximately 2.4 km intervals and the vessels were, on average, 260 m apart during tows. The range of volumes filtered by net and tow type was 505-560 m^3 for a 70 cm net in oblique tow; 244-307 m^3 for a 70 cm net in surface tow; 4,600-5,650 m^3 for a 2 m net in oblique tow; and 3,600 m^3 for a 2 m net in surface tow. Mean displacement volume of plankton caught by the 70 cm net was higher in oblique tows (27.3 mL/1,000 m^3) than in surface tows (4.4 mL/1,000 m^3). Both surface and oblique tows with the 70 cm nets caught a total of 283 tuna larvae whereas the 2 m nets caught 123 (Table 2). The species composition of the sorted and identified catches was similar except for an unidentified component in the CSIRO catches. This was due to a more conservative approach to identification by the less experienced CSIRO staff. The species composition of the FSFRL samples suggests that most CSIRO *Thunnus* spp. were probably *Thunnus alalunga*.

TABLE 2.—Numbers of tuna larvae taken in 2 m net hauls (surface and oblique) by FRV *Shoyo Maru* and in 70 cm net hauls (surface and oblique) by FRV *Soela*.

	2 m net		70 cm net	
Species	*n*	%	*n*	%
Thunnus maccoyii	9	(7.3)	21	(7.4)
Thunnus obesus	3	(2.4)	0	(0)
Thunnus albacares	7	(5.7)	0	(0)
Thunnus alalunga	77	(62.6)	78	(27.6)
Thunnus albacares/alalunga	25	(20.0)	66	(23.3)
Katsuwonus pelamis	1	(0.8)	1	(0.4)
Thunnus spp.[1]	0	(0)	117	(41.3)
Total	123		283	

[1]Small larvae 2.1–3.8 mm SL but usually < 3.3 mm SL not having the pigment pattern needed to distinguish to species.

The mean catch in the 70 cm net in oblique and surface tows was 16.5 and 144.7 tuna larvae/1,000 m^3, respectively. Catches in the 2 m net in oblique and surface tows were much lower, 1.4 and 3.7 tuna larvae/1,000 m^3, respectively. The ratio of the mean catches (70 cm net/2 m net) was 11.8 (SE ± 3.5) for oblique tows and 39.6 (SE ± 10.7) for surface tows. Catches in the 70 cm net were significantly higher than in the 2 m net ($F = 140.9$; df = 1,5; $P < 0.001$) and catches in surface tows were significantly higher than oblique tows ($F = 11.3$; df = 1,10; $P < 0.01$). The difference in catch between surface and oblique tows was mainly attributable to the 70 cm net; hence, there was a significant interaction between net type and tow depth ($F = 6.1$; df = 1,10; $P < 0.05$) (Fig. 2).

There were significant differences in the mean lengths of larvae caught by net and tow type (Kruskal-Wallis test; $H = 21.74$; df = 3; $P < 0.001$). The mean length of tuna larvae caught in the 2 m oblique tows (4.03 mm) was significantly greater (Dunn test; $P < 0.05$) than those caught in 2 m surface tows (3.60 mm), 70 cm oblique tows (3.56 mm), and 70 cm surface tows (3.65 mm) (Fig. 3). This was due to a lower proportion of small larvae (and the absence of larvae less

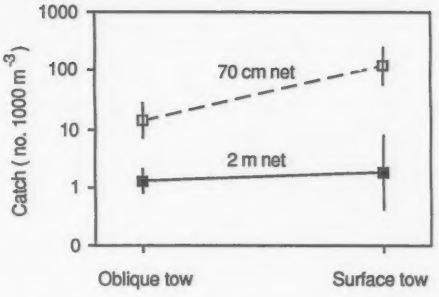

FIGURE 2.—Geometric mean catch (1,000 m^{-3}) by the 70 cm and 2 m net in surface and oblique tows and 95% confidence intervals. Catch has been plotted on a log scale.

than 3.0 mm) rather than an increased proportion of large larvae in the 2 m oblique tow (Fig. 3).

Discussion

No attempt was made to control the many variables that could contribute to the difference in abundance estimates of the two sampling programs; we were more interested in the relative effectiveness of existing methods rather than in the effects of specific variables. CSIRO estimates based on surface and oblique tows were 93 and 13 times greater than corresponding estimates by FSFRL. The most obvious and

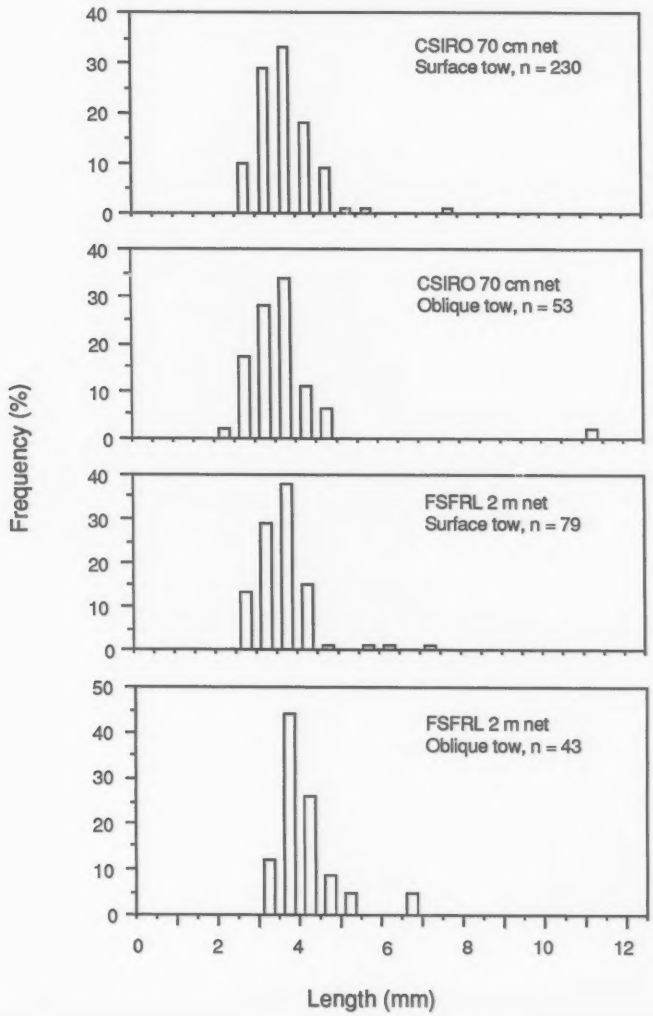
CSIRO 70 cm net
Surface tow, n = 230
CSIRO 70 cm net
Oblique tow, n = 53
FSFRL 2 m net
Surface tow, n = 79
FSFRL 2 m net
Oblique tow, n = 43
Frequency (%)
Length (mm)

FIGURE 3.—Length-frequency distribution of tuna larvae caught in 2 m net hauls (surface and oblique) by FRV *Shoyo Maru* and in 70 cm net hauls (surface and oblique) by FRV *Soela*.

arguably the most important difference between the nets used by the programs is that the FSFRL 2 m net has 1.7 mm mesh in the forward section. Larvae are apparently lost by mesh escapement through this section. This type of multimesh construction may "herd" the larvae, but this advantage seems to be greatly outweighed by escapement. If we assume that the 1.7 mm mesh retains no larvae, then catches by the 2 m net can be recalculated for the 1.05 m diameter opening of the remaining 0.5 mm mesh section. This gave mean catches of 12.3 and 5.09 larvae/1,000 m^3 for surface and oblique tows, respectively. Based on this assumption, the CSIRO catches were still 12 times larger than FSFRL catches for surface tows and about 3 times greater for oblique tows. Reanalysis of the ANOVA using these data produced the same differences and levels of significance as in the original analysis. This demonstrates that, although escapement through the 1.7 mm mesh may account for a significant loss of larvae, other factors must also contribute to the lower catches by the FSFRL program.

A number of factors could cause increased avoidance of the 2 m net and hence reduce catches. While it might be expected that the 2 m net would reduce net avoidance by virtue of its size, this may have the opposite effect owing to an increase in the reaction distance to it (Barkley 1964, 1972; Wiebe et al. 1982). It has been well established that samplers that have no bridle obstructing the mouth (such as bongo nets and the 70 cm net) are far more efficient samplers than nets with conventional triple-rigged bridles (such as the 2 m net) owing to increased avoidance of the latter (Posgay and Marak 1980). Other factors that could increase avoidance of the 2 m net include the 30 kg depressor attached directly to the frame of the net, increasing visibility and turbulence and hence the reaction distance, and the high visibility of the undyed (white) net compared with the blue 70 cm net (Smith and Richardson 1977).

The volume filtered by the 2 m net may also have been overestimated as it was measured outside the net by the depth/distance recorder. This would result in lower apparent catch rates. Reduced filtering efficiency due to clogging in the 0.5 mm section, which may be a problem with the 2 m net because of its low open area ratio (Tranter and Heron 1967), would not be detected. In the laboratory, the sorting of larvae from samples without the aid of a microscope could result in extraction of fewer larvae in the FSFRL program, thus further reducing apparent catches.

The 70 cm net caught greater numbers of tuna larvae in the surface tow relative to the oblique tow than did the 2 m net. Catches in the 2 m net surface tow may have been reduced by increased avoidance because the net is towed very close to the hull of the *Shoyo Maru*. Alternatively, the oblique tow may have oversampled surface waters where the larvae are more abundant. The tow profiles for the 2 m oblique tow do suggest that this occurred to some extent. Clogging of the 0.5 mm mesh in the surface tows would not account for the disproportionately low catches because clogging would have been more likely to occur in the oblique tows which caught greater volumes of plankton.

We are not sure of the reasons for the differences in lengths of larvae caught by the two programs because of the many possible confounding factors. The greater mean length of larvae in the FSFRL oblique tows was due to fewer small larvae rather than to greater catches of large larvae. This could have resulted from differences in net deployment or in processing of samples, or could simply have been an artifact of the small sample size collected by the 2 m net in oblique tows. It would not have been due to differential loss of small larvae through the 1.7 mm mesh because this did not occur in surface tows with the same net.

The estimated abundance of tuna larvae in CSIRO surface and oblique tows was much higher than the corresponding estimates by the FSFRL program. We assume that larger catches are more accurate than smaller catches because towed nets are inefficient samplers owing to avoidance and mesh escapement (Clutter and Anraku 1968; Murphy and Clutter 1972; Clarke 1983) and subsequent treatment of samples (removal from nets, sorting, and enumeration) is likely to lead to the loss of larvae resulting in underestimation rather than overestimation. This would suggest that the 70 cm net as it is deployed in the CSIRO program is more efficient at catching tuna larvae than the 2 m net used in the FSFRL program, despite its much smaller size.

Acknowledgments

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Longbill Spearfish, *Tetrapturus pfluegeri*, Incidentally Caught by Recreational Billfishermen in the Western North Atlantic Ocean, 1974–86

Recreational billfish surveys have been conducted annually by the National Marine Fisheries Service (NMFS), Southeast Fisheries Center (SEFC), in the Atlantic Ocean off the U.S. east coast, the Gulf of Mexico, the Bahamas, and the Caribbean Sea since 1971. During these surveys, biological samples were collected to determine age and growth parameters, and reproductive biology; and to monitor catch and effort trends of all billfish species. These species include the sailfish, *Istiophorus platypterus*, white marlin, *Tetrapturus albidus*, blue marlin, *Makaira nigricans*, and longbill spearfish, *Tetrapturus pfluegeri*. With the exception of the longbill spearfish, these species have received considerable attention from fisheries scientists (Nakamura 1985). Owing to the rarity of longbill spearfish in coastal waters, there have been very little fisheries information and biological data published (Robins 1975; Nakamura 1985). All spearfish data collected by the NMFS/SEFC during the annual recreational billfish surveys are summarized in this note.

The longbill spearfish is an epipelagic species found in offshore waters throughout the Atlantic Ocean extending from lat. 40°N to 35°S (Nakamura 1985). These fish are commonly caught by foreign longline vessels fishing offshore for tuna (Ueyanagi et al. 1970) but are rarely caught by recreational vessels fishing closer inshore for sailfish and marlin (Beardsley and Conser 1981). Longbill spearfish are incidentally caught by recreational fishermen while trolling for the more popular sailfish and marlin.

Spearfish are caught during the months of March through September, but particularly during the summer (Fig. 1). The shortened seasons for catches in the temperate Gulf of Mexico and Atlantic, contrasted with the extended season in the tropical Caribbean, indicate that spearfish prefer warm offshore water. The fish were caught during daylight, with the majority being caught between the hours of 0800 and 1400 (Table 1). Spearfish feed on a variety of epipelagic organisms (Ovchinnikov 1979). Limited data (29 specimens) showed no distinct preference for either artificial or natural (dead) trolled baits (Table 1).

The average length and weight of the spearfish was 151.8 cm (lower jaw fork length, SD 24.3, $N = 35$) and 14.7 kg (SD 6.3, $N = 38$). These lengths and weights are similar to the

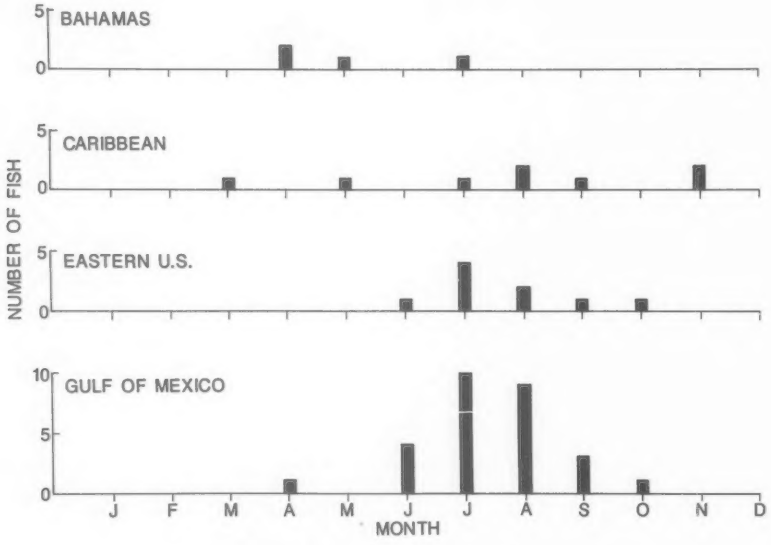

FIGURE 1.—Seasonality, by geographic area, of spearfish observed during annual NMFS/SEFC recreational billfish surveys, 1974–86.

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Fishery Bulletin, U.S. 87: 982–984, 1989.

TABLE 1.—Fishery and biological data of spearfish caught during the annual NMFS/SEFC recreational billfish surveys, 1974–86.

Fisheries parameter	Number caught	Percent (%)
Time		
0600–0800	2	4.8
0801–1000	10	23.8
1001–1200	9	21.4
1201–1400	16	38.1
1401–1600	4	9.5
1601–1800	0	0.0
1801–2000	1	2.4
Total	42	100.0
Bait		
Artificial	12	41.2
Natural (deed)	10	34.5
Combination	7	24.3
Total	29	100.0
Sex		
Male	12	60.0
Female	8	40.0
Total	20	100.0

figures reported by Robins (1975) for recreationally caught spearfish in Florida and are considerably smaller than the reported maximum length of 200 cm and weight of 45 kg (Nakamura 1985). The length:weight relationship of 34 spearfish observed is given in Figure 2. Also, there is no notable sexual dimorphism reflected in the spearfish length-weight relationship (Fig. 2) as reported in other billfish species (Nakamura 1985). This, however, may be an artifact of the small sample size.

The determination of an accurate sex ratio is difficult owing to the small sample size (Table 1) and the large time frame and geographic area from which these data were collected. Of the 20 fish that were reliably sexed, 12 were male and 8 were female; this indicates a male to female ratio of 1:0.66, compared with the 19 specimens and 1:1 ratio observed by Robins (1975) in the Florida recreational billfish fishery. When the two data sets are aggregated to form a larger sample size of recreationally caught spearfish, these data provide a ratio of 1:0.80. Interestingly, Ueyanagi et al. (1970) reported that 106 male and 62 female spearfish were incidentally captured by Japanese tuna longline vessels in the

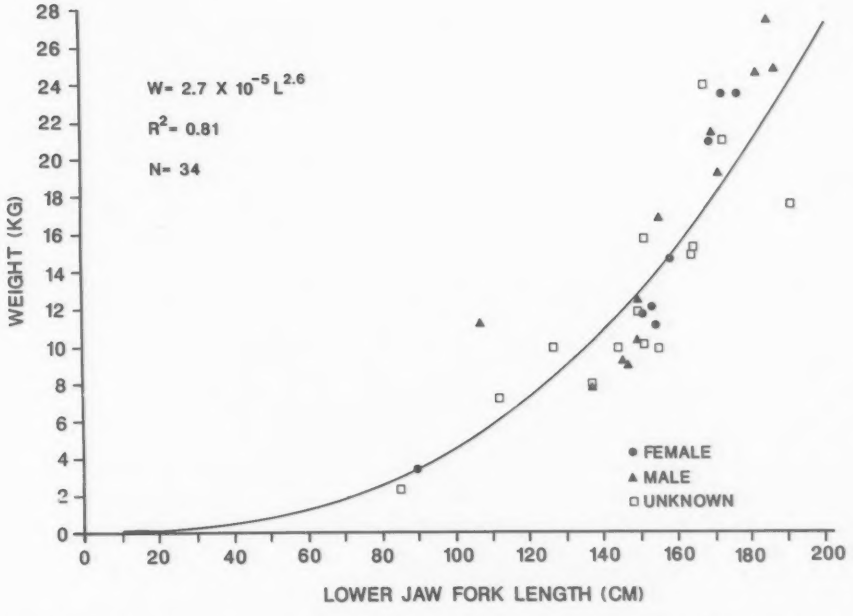

FIGURE 2.—Length:weight relationship of spearfish observed during annual NMFS/SEFC recreational billfish surveys, 1974–86.

western north Atlantic at a ratio of 1:0.58. This suggests that the recreationally derived sex ratios may, in fact, be realistic.

The catch of recreationally caught spearfish varies temporally and spatially (Table 2), with an overall value of 0.00869 fish caught per 100 hours. The Caribbean produced the highest CPUE for spearfish followed by the Gulf of Mexico, the eastern United States, and the Bahamas.

TABLE 2.—Catch and effort (expressed as hours fished) data of spearfish caught during annual NMFS/SEFC recreational billfish surveys, 1974–86.

Year	Gulf of Mexico catch/effort	Eastern U.S. catch/effort	Caribbean catch/effort	Bahamas catch/effort	Total catch/effort	CPUE[1]
1974	1/11,005	0/ 8,728	0/ 3,935	0/ 6,711	1/30,379	0.00329
1975	2/15,060	0/10,949	0/ 3,809	0/ 5,879	2/35,697	0.00560
1976	1/ 8,904	0/ 9,077	0/ 2,844	1/ 5,283	2/26,148	0.00764
1977	3/11,600	0/11,070	0/ 2,473	0/ 5,200	3/30,343	0.00988
1978	9/31,905	1/11,429	0/ 4,156	1/ 5,606	11/53,096	0.02071
1979	3/10,960	0/ 9,351	0/ 676	0/ 6,383	3/27,370	0.01096
1980	0/13,312	2/22,140	0/ 236	0/ 8,041	2/43,729	0.00457
1981	4/15,525	0/16,720	0/ 2,182	1/10,688	5/45,115	0.01108
1982	1/ 8,863	0/ 8,504	0/ 2,251	0/ 9,710	1/29,328	0.00340
1983	0/13,304	2/34,169	6/19,148	0/11,441	8/78,062	0.01024
1984	2/14,524	2/28,520	0/ 9,675	1/16,014	5/68,733	0.00727
1985	1/12,599	0/12,140	1/11,845	0/12,071	2/48,655	0.00411
1986	1/10,604	2/19,204	1/ 3,735	0/13,588	4/47,133	0.00848
Total	28/178,165	9/202,001	8/67,005	4/116,615	49/563,786	0.00869
CPUE	0.01571	0.00445	0.01193	0.00343	0.00869	

[1]CPUE = Number of spearfish caught per 100 hours fished.

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Age Determination in Larval and Juvenile Sheepshead, *Archosargus probatocephalus*

Pannella (1971) first demonstrated the existence of daily growth increments in the otoliths of several species of teleosts. Enumeration of these daily increments is particularly useful for age determination in larval and juvenile fishes. Verification of daily growth rings in individual fish species has generally been approached in one of two ways: laboratory rearing (Brothers et al. 1976; Struhsaker and Uchiyama 1976; Taubert and Cable 1977; Barkman 1978; McGurk 1984; Davis et al. 1985;) or by using chemical marking techniques either in the wild or in the laboratory. Oxytetracycline hydrochloride has been used to produce a fluorescent mark for examination of daily growth increments in otoliths of the starry flounder, *Platichthys stellatus* (Campana and Neilson 1982), and juvenile Hawaiian snapper, *Pristipomoides filamentosus* (Ralston and Miyamoto 1983). Otolith microstructure and its use in fish age determination was reviewed by Campana and Neilson (1985).

The early life history of the sheepshead, *Archosargus probatocephalus*, is poorly known. In this study, daily growth rings in the otoliths of larval and juvenile sheepshead were examined and validation was accomplished using tetracycline-marked specimens held in the laboratory. The daily rings of wild caught specimens were counted to obtain information on the age at transition from larva to juvenile.

Materials and Methods

Sheepshead larvae and juveniles were collected from Bayboro Harbor, St. Petersburg, FL, between 21 April 1983 and 7 May 1985. Larvae (5–8 mm SL) and juveniles (greater than about 8 mm) were collected from a seawall using a dip net fished at the surface. All specimens were preserved in 95% ethanol. Subsamples of larvae were measured (SL) using an ocular micrometer, and the sagittal otoliths were teased out and mounted on microscope slides using Pro-texx[1] mounting media. In the largest individuals (about 10 mm SL), one otolith was mounted on a microscope slide in thermoplastic cement and polished with 3 μ grit microtome paper. The otoliths were polished until the rings near the primordium were clearly visible (Fig. 1).

The daily nature of the growth increments was validated using 29, (7–10 mm SL) wild-caught larvae collected on 1 May 1984. Larvae were placed in 38 L aquaria containing oxytetracycline hydrochloride at a concentration of 10–15 mg/L, left for 7 hours, and then were removed to untreated tanks. Fish were fed *Artemia salina* nauplii and allowed to grow for 6 or 15 days, after which they were preserved in 95% ethyl alcohol and stored in the dark. The position of the tetracycline mark was determined by preparing these otoliths as described above and alternately viewing them under ultraviolet and visible light.

Otoliths were examined at 630–1000× magnification using a compound microscope equipped with a high resolution closed circuit television to improve contrast. Daily growth increments were independently counted by two readers. Counts were considered in agreement if they differed by two or less increments. When the counts differed by two increments, the median value was used; when they differed by one increment, the greater value was used. If counts differed by three or more, those otoliths were reexamined by both readers in a joint effort to resolve the differences. About 5% of the otoliths were excluded from the data set because differences in counts could not be resolved.

Results

Approximately 2,000 larval and juvenile sheepshead, ranging in size from about 5–10 mm, were collected during the study (Fig. 2). About 90% of the individuals were 6.5–8.0 mm (mean = 7.0 mm); fish larger than approximately 8 mm represented less than 2% of the sample. Rings in otoliths of larval and juvenile sheepshead were clear (Fig. 1), and results of the validation experiment confirmed daily increment formation, at least between 7 and 10 mm. Of 26 specimens sacrificed six days after tetracycline treatment, 19 showed clear marks and had produced six increments beyond the reference mark. Reference marks could not be located on six of the remaining specimens, and the increments could not be counted on one specimen. The specimens sacrificed after 15 d post-treatment showed clear reference marks and had produced 15 increments.

A sample of 129 larval and juvenile sheeps-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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Fishery Bulletin, U.S. 87:985–988, 1989.

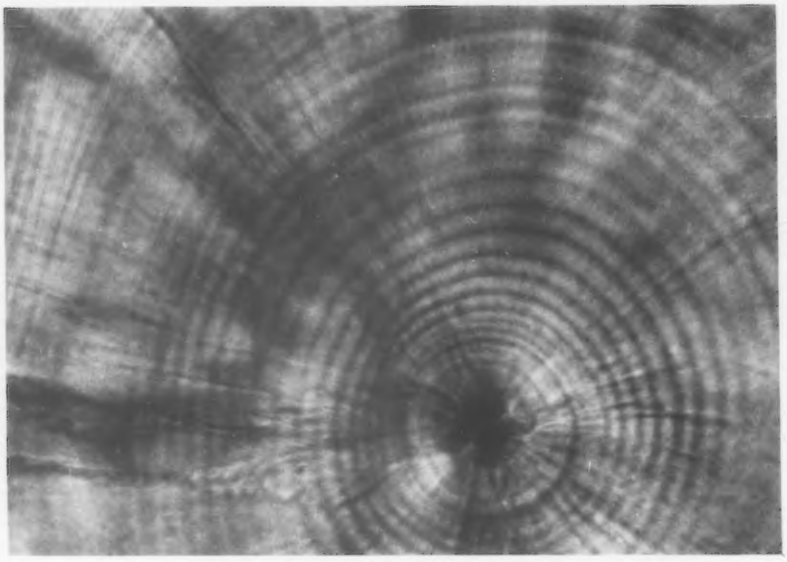

FIGURE 1.—Photomicrograph through the central region of an otolith taken from a 10.5 mm sheepshead (80× magnification). This otolith was polished to increase ring clarity.

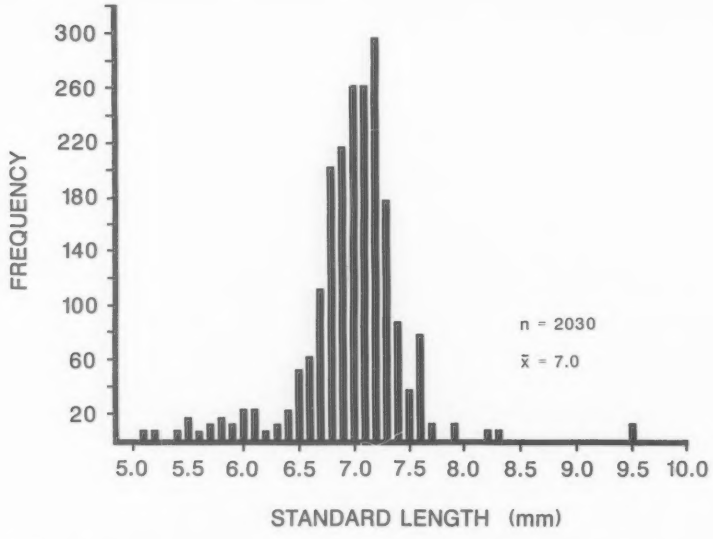

FIGURE 2.—Length-frequency distribution of all sheepshead collected by dip net from the Bayboro Harbor site.

head (5.1–10.5 mm SL) were aged. First increment formation was assumed to begin at hatching such that the otolith age equals the "real" age. Of this sample, 93 specimens were taken from field collections, the remainder were tetracycline treated individuals held in the laboratory. Figure 3 shows the results of these age determinations.

Discussion

Once daily periodicity in increment formation was validated in sheepshead otoliths through the use of tetracycline marking, it was possible to determine the timing of life history transitions. The time required for transition from larval to juvenile stage has been determined for a number of species (Brothers et al. 1983; Campana 1984). The data presented in Figure 2 indicate that by about 8 mm SL most sheepshead larvae have disappeared from dip net collections. This coincides with the size at beginning of transformation as reported by Mook (1977). The disappearance of larvae from collections may reflect their ability to avoid capture or their movement out of the pelagic environment, both facilitated by increased swimming ability acquired after metamorphosis. Sheepshead are substrate-oriented fish, and a "settling" of larvae may occur at metamorphosis. Using the data presented in Figure 3, the minimum and maximum age of an 8 mm fish can be roughly estimated at about 30 and 40 days, respectively. If daily increment formation begins at hatching (see Brothers et al. [1983] for a discussion of this assumption) then the pelagic stage of the sheepshead under the environmental conditions of Bayboro Harbor is between about 30 and 40 days. Other species possessing similar ages/sizes at transition include the spot, *Leiostomus xanthurus*, which transforms at 8 mm after 40 days (Fahay 1983; Warlen and Chester 1985) and the Atlantic croaker, *Micropogonias undulatus*, which transforms at 10 mm after 60 days (Fahay 1983; Joann Lyczkowski-Shultz[2]. The results presented here suggest that sheepshead larvae develop more slowly than the larvae of the closely related sea bream, *Archosargus rhomboidalis*. Sea bream larvae reared in captivity began transformation at the same size as sheepshead (8 mm) but only 15 days after hatching (Houde and Pothoff 1976). It is noteworthy that five sheepshead larvae (7.9–8.1 mm), held in the laboratory during tetracycline treatments, were found to have a mean age of 36.8 days (range = 35–38 days) (Fig. 3). These comparisons must be cautiously interpreted, however, because growth acceleration or retardation may occur in captivity.

Acknowledgments

I would like to thank the employees of the Florida Department of Natural Resources,

[2]J. Lyczkowski-Shultz, Gulf Coast Research Laboratory, P.O. Box 7000, Ocean Springs, MS 39564, pers. commun. March 1989.

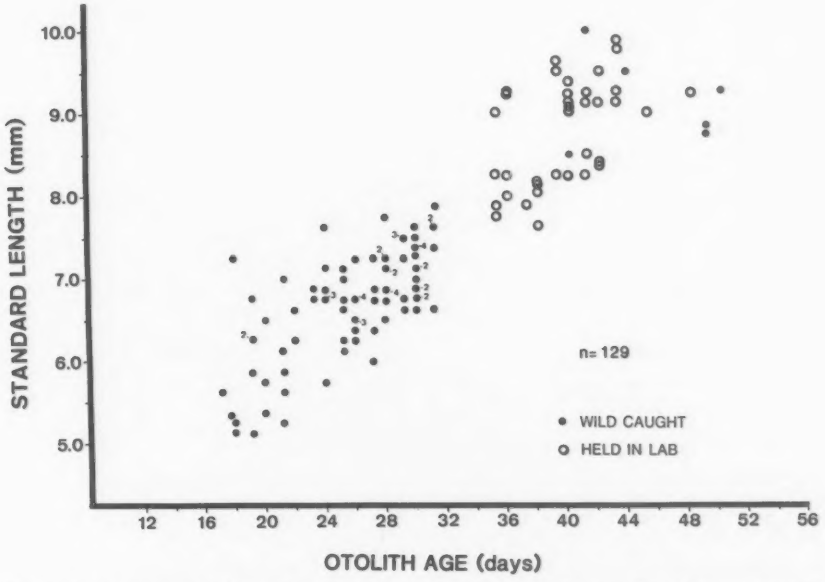

FIGURE 3.—A scatter plot of length on age for larval and early juvenile sheepshead between 5 and 10 mm SL.

Marine Research Laboratory, particularly L. Bullock, J. Gartner, M. Leiby, B. McMichael, M. Murphy, and R. Taylor. I would also like to thank E. Peebles and G. Tolley for reviewing the manuscript.

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Reproductive Status of Dover Sole, *Microstomus pacificus*, off Northern Oregon

Dover sole, *Microstomus pacificus*, range latitudinally from northern Baja California to the Bering Sea (Hart 1973) but are commercially abundant only from central California to British Columbia. They inhabit a wide depth range, from shallow, inshore waters (juveniles) to at least 1,000 m. Maximum recorded size is 71 cm total length (Hart 1973). On the basis of biomass, Dover sole is the most abundant species of flatfish landed commercially off Oregon (Demory et al.[1]) and dominates the Columbia Slope Assemblage (located at depths >220 m) described by Gabriel and Tyler (1980). Landing and effort statistics for this species in the International North Pacific Fisheries Commission (INPFC) Columbia Area (lat. 43°00′–47°30′N) were relatively stable for the 20 years prior to 1977, but have since almost tripled (Demory et al[2]).

From data extending back to 1951, Demory et al. (fn. 2) suggested a decline in age-specific length for this species during the last several years (mean length at age 10 years was about

[1]Demory, R. L., M. S. Hoxie, N. TenEyck, and B. O. Forsberg. 1976. Marine resource surveys on the continental shelf off Oregon, 1971–74. Unpubl. rep. Oreg. Dep. Fish Wildl., Newport, OR 97365.

[2]Demory, R. L., J. T. Golden, and E. K. Pikitch. 1984. Status of dover sole (*Microstomus pacificus*) in INPFC Columbia and Vancouver areas in 1984. Unpubl. rep. Oreg. Dep. Fish Wildl., Newport, OR 97365.

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Fishery Bulletin, U.S. 87:988–995, 1989.

43.5 cm, 42.3 cm, and 38.3 cm in 1951, 1965, and 1982, respectively). Because fecundity is proportional to size, this decline implies that the reproductive capacity of the stock has decreased (Bagenal 1973; Borisov 1979), provided that relative fecundity or size and age at first maturity have not undergone compensatory changes. Data on fecundity and state of maturity of Dover sole off Oregon have not been collected since 1950 (Harry 1959).

In this paper, we describe fecundity of Dover sole from the Columbia area during the 1985–86 spawning season as a function of length, weight, and age, and compare the relationship between length and fecundity with that previously estimated from fish collected between 1948 and 1950 in the same geographical area (Harry 1959). Size and age at maturation are also assessed and compared with the limited information presented by Harry (1959).

Materials and Methods

Samples for estimating fecundity were obtained from commercial trawlers fishing off northern Oregon (about lat. 46°N) during December 1985. Fish total length (TL, nearest mm) was measured and both otoliths were removed and stored in 50% ethanol for age determination. Ovaries were preserved in a 10% phosphate-buffered formaldehyde solution. Maturity stages were assigned using macroscopic inspection of ovaries and oocytes and applying criteria described by Hagerman (1952). Comparable criteria were used by Harry (1956). Because most specimens were filleted prior to sampling, the relationship between total length and ovary-free body weight (nearest 0.1 g) was established from intact fish collected at the same time. Body weight at length for filleted fish was estimated from this relationship. Additional specimens (collected from 44° to 45°N) were sampled in December 1985 and January 1986 from processing plants in Newport, OR and used to describe state of maturity. Total length was measured and otoliths were removed.

Oocyte counts for fecundity estimates were made using the gravimetric subsampling method for MacGregor (1957), as described by Hunter et al. (1985). Both ovaries preserved from each fish were blotted dry and weighed to the nearest 0.1 g. Three subsamples of oocytes were removed from each fish (one each from the anterior, middle, and posterior regions of one ovary, either left or right). Subsamples were weighed to the nearest 0.1 mg, placed on microscope slides in 33% glycerin, and teased apart to form one layer of oocytes. Minimum and maximum diameters of mature, yolked oocytes were estimated from each subsample. Subsamples weighed between 30 and 80 mg, and contained about 100–300 oocytes.

Ovaries were advanced enough to allow discrimination of large, mature oocytes from smaller partially-yolked oocytes and non-yolked oocytes by the unaided eye. Oocyte size-frequency distributions were determined microscopically from the ovaries of 10 fish (MacGregor 1957). Using a Zeiss Videoplan II[3] image analyzer, and a dissecting microscope with camera lucida attachment, approximately 250 oocytes lying along transect lines etched in the microscope slide were measured to the nearest micron, and size-frequency distributions were evaluated. The modal size group of advanced oocytes was determined by visual inspection of the size-frequency plots. An average minimum size-threshold for oocytes associated with the most advanced and distinct modes in these 10 plots was determined. Ovaries with advanced oocytes that all exceeded this size-threshold were used in estimating fecundity. Individual fecundity was calculated by multiplying total ovarian weight by mean number of advanced oocytes per mg in the three subsamples.

Age was determined for each fish used in estimating fecundity and for a subsample of those fish used for maturity assessment. The left otolith was prepared and sectioned as described by Boehlert and Yoklavich (1984). Annuli were counted on a dissecting microscope at 80× magnification using reflected light and a black background. Age was determined twice for each fish, approximately one month apart, to establish precision of the age estimate. There was no difference between the two age determinations for each of 75 fish (paired t-test, $P > 0.50$). The first estimate was used in further analyses. There has been no age validation for Dover sole, but similar methods have accurately aged other long-lived species (*Sebastes diploproa*, Bennett et al. 1982; *A. fimbria*, Beamish et al. 1983; *S. flavidus*, Leaman and Nagtegaal 1987).

Results

To determine fecundity, 97 ovaries were col-

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

lected during the first two weeks of December 1985. Eighteen ovaries were spent, while the others were classified as mature ovaries, full of developing oocytes that were distinguishable by the unaided eye. Fifty-seven of the mature ovaries, from fish 345 to 550 mm TL, were used for fecundity assessment; ovaries of the remaining 22 fish were either poorly preserved or not intact. No hydrated or translucent oocytes were evident in the ovaries used for fecundity. Size-frequency distributions of oocytes from 10 mature, prespawning fish were generally bimodal (Fig. 1). Seven of these ovaries had distinct modes of advanced oocytes; from these

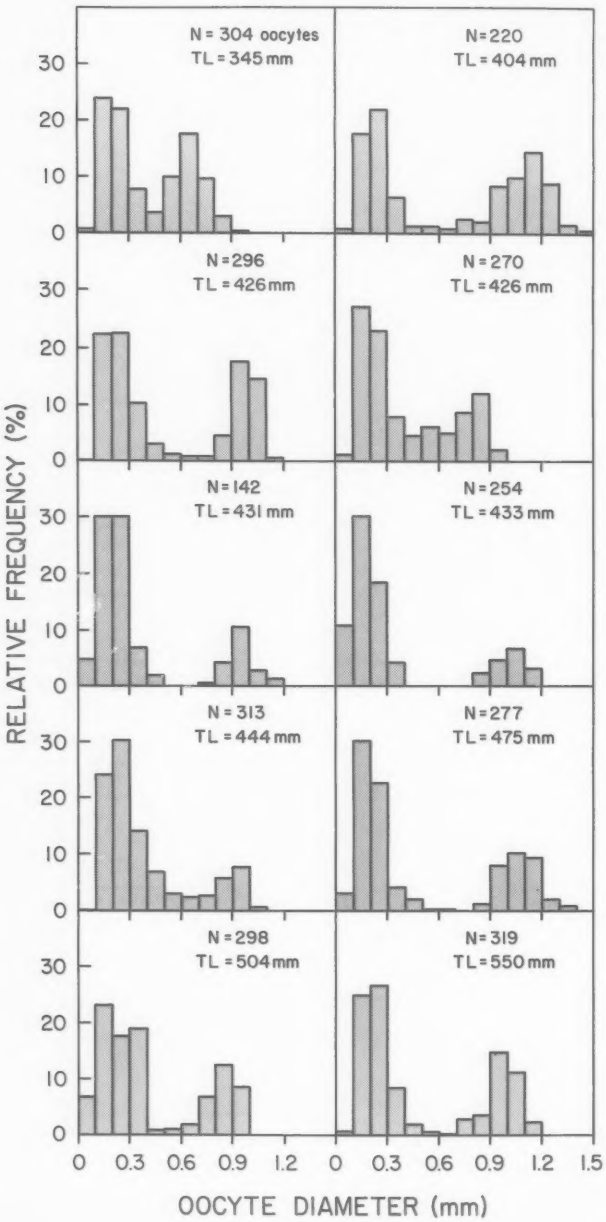

FIGURE 1.—Size-frequency distributions of oocyte diameter from ovaries of 10 Dover sole. Total length of fish and number of measured oocytes are indicated.

distributions, the mean minimum size was 0.65 mm for advanced, yolked oocytes to be used in fecundity estimates. The largest measured oocytes were 1.45 mm in diameter.

The number of advanced, yolked oocytes (≥0.65 mm in diameter) per mg of tissue was calculated for each of three subsamples from 32 of the 57 ovaries. The coefficient of variation ranged from 0.1 to 9.1%, with a mean of 4.0%. This range is comparable to that found when enumerating the eggs of sablefish, *Anoplopoma fimbria*, (Mason et al. 1983) and widow rockfish, *Sebastes entomelas*, (Boehlert et al. 1982).

Fecundity of Dover sole ranged from 39,748 to 167,046 oocytes. As expected, fecundity increased with increasing length of fish (Fig. 2); this relationship was best described by the following power equation, using nonlinear, least squares regression methods:

$$F = (1.637 \times 10^{-6})L^{4.02} \qquad r^2 = 0.82,$$

where F is fecundity (total number of advanced oocytes per fish), L is total length of fish (mm), and r^2 is the coefficient of determination.

We found no statistical difference between the fecundity-length relationship from Dover sole collected by Harry (1959) and those reported here. A linear, least squares regression of our logarithmically transformed length-specific fecundity data was compared with an analogous function we derived from Harry's data, for lengths of fish common to both studies (425–550 mm TL; Fig. 2). Neither slopes (t-test, $P > 0.510$) nor intercepts (t-test, $P > 0.078$) of the regression lines differed significantly. The proportion of the total variation in fecundity that is accounted for by the fitted regression ($r^2 = 0.82$ in the present study and $r^2 = 0.75$ in Harry (1959)) is typical for many species of fish and reflects variable body weight, nutritional condition, age, and possible onset of spawning (Bagenal 1973; Hempel 1979).

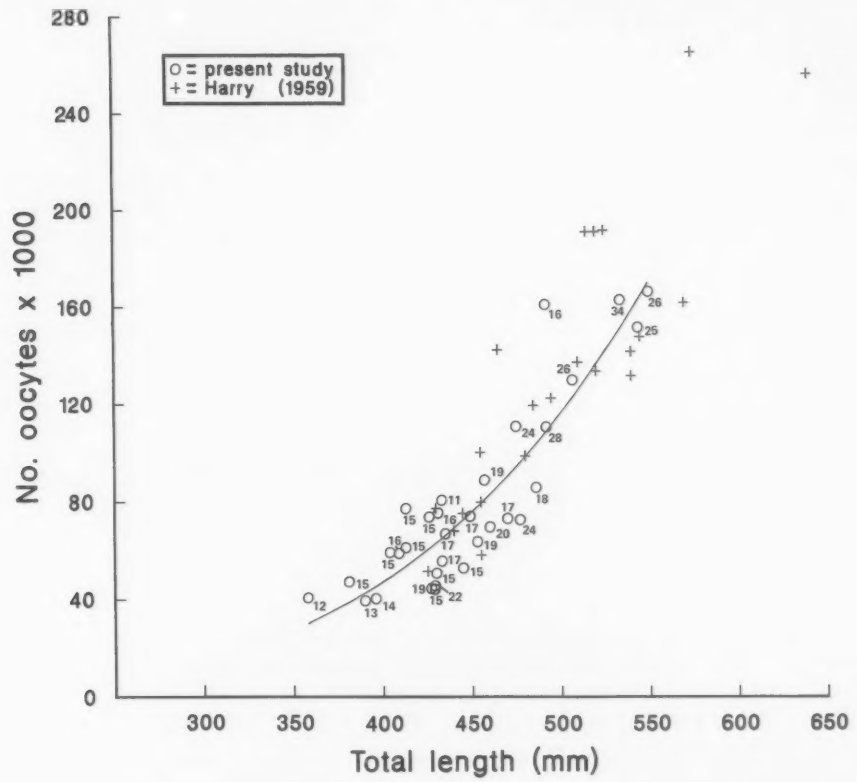

FIGURE 2.—Fecundity of Dover sole relative to total length. Open circles represent fecundity from present study (N = 32) and line is the predicted relationship through these points ($F = 1.637 \times 10^{-6} L^{4.02}$). Crosses represent fecundity estimated by Harry (1959; N = 22). Number adjacent to open circle indicates age of female.

Ovary-free body weight (W; 185–1,490 g) and total body length (L; 287–550 mm) from a sample of 115 female Dover sole were fit with a nonlinear, least squares power function:

$$W = (3.34 \times 10^{-6})L^{3.147} \qquad r^2 = 0.96.$$

Ovary-free body weight was subsequently estimated from total length for those Dover sole that were filleted prior to sampling. Fecundity was expressed as a linear, least squares function of ovary-free body weight, resulting in the fitted equation:

$$F = 133.4W - 21{,}890.3 \qquad r^2 = 0.81$$
$$N = 32,$$

where N is number of ovaries. Although weight was estimated from total length of fish, this fitted equation is adequate because the variance of errors associated with estimated weight is very small when compared with the variance in the weights themselves (Draper and Smith 1981, p. 124). Weight-specific fecundity averaged 102.4 eggs/g ovary-free body weight (SD = 22.0, N = 32).

The Dover sole used for determining fecundity were 11–34 years of age. Fecundity and age were not as strongly correlated as fecundity and length or weight, yet fecundity generally increased with increasing age (Fig. 2). The relationship between fecundity and age, from the 32 fish evaluated in this study, was best fit by a nonlinear, least squares exponential function:

$$F = 25{,}080\, e^{(0.0586A)} \qquad r^2 = 0.65,$$

where A is age of the fish in years.

Stage of maturity was determined for 370 female Dover sole, ranging in size from 235 to 489 mm TL (Fig. 3). Because samples were collected from processing plants, many small fish had been discarded at sea and were poorly represented. Emphasis was placed on obtaining information from fish below fillet size (320 mm TL). Nearly 99% of the fish examined were classified as sexually mature; 67.2% of these were spent, and 32.5% contained ovaries with advanced, yolked oocytes that were clearly discernible upon macroscopic inspection. Only four fish (305–318 mm TL) were immature, and one fish was in a resting stage. Advanced oocytes occurred in fish of all lengths. This relationship suggests that fish were maturing at a much smaller size than that reported by Harry (1959; Fig. 3). State of maturity seems to be dependent on the size of the fish. Frequencies of fish in five 5 cm length groups (24–28; 29–33; 34–38; 39–43; and 44–48 cm) and in two states of maturity (advanced oocytes and spent ovaries) were arranged in a 2 × 5 contingency table; the independence of total length and state of maturity was tested. Significantly more of the small fish were spent (Chi-square = 78.76; $P <$

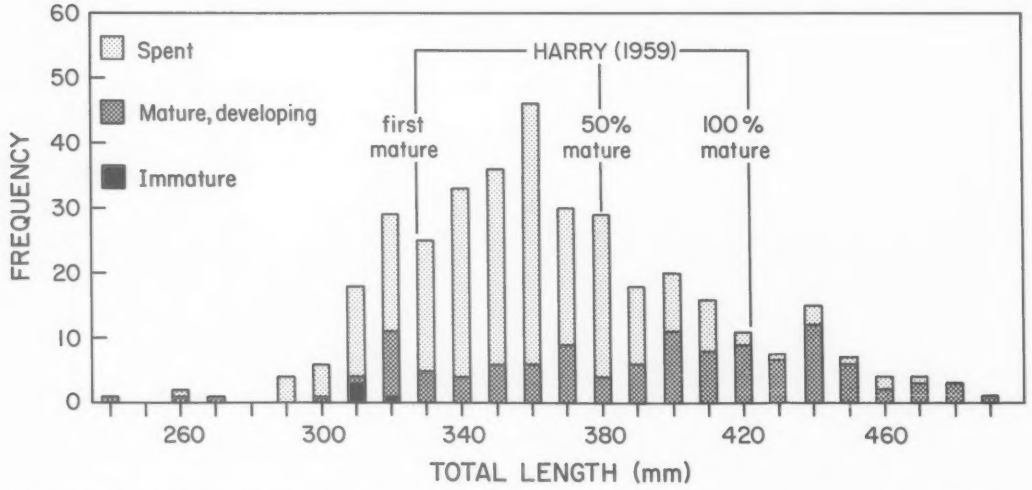

FIGURE 3.—Length frequency of 370 female Dover sole at three stages of maturity. Comparative information from Harry (1959) is indicated.

0.001); smaller fish appear to have an earlier, and possibly shorter, spawning season. Preliminary data on Dover sole collected in California indicated that larger fish still contained eggs in late spring (Hunter[4]), thus supporting our findings.

From those fish assessed for state of maturity, a subsample of 162 was selected for age determination. All were mature; 78% were spent, and 22% contained advanced, yolked oocytes. Fish were 5–24 years old (Fig. 4). As expected from the length at maturity analysis, most (77.1%) of the 35 fish with advanced oocytes were older than 10 years of age; 53.5% of the spent fish were older than 10 years.

Discussion

One cannot conclude unequivocally that the estimated number of advanced oocytes prior to spawning corresponds to reproductive output of Dover sole, owing to incomplete spawning events or resorption of oocytes (Foucher and Beamish 1980). In addition, considering that 20% of the females collected for fecundity estimates during December were spent, some fish with advanced ovaries may have partially spawned. If so, fecundity would have been underestimated for those fish. We maintain that our data reflect the potential fecundity of Dover sole for the following reasons: 1) oocyte size distributions did not demonstrate a distinct spawning batch (oocyte diameter >1.80 mm), suggesting that these females had not yet spawned; 2) no hydrated oocytes were observed in the ovaries used for fecundity estimates, although hydration could occur rapidly and therefore its absence could be a sampling artifact; and 3) our coefficients of determination for regressions of fecundity on length and on weight are relatively high ($r^2 = 0.82$ and 0.81, respectively); if a significant number of oocytes had been released, variability could have conceivably been much greater. An additional source of underestimation

[4]J. Hunter, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA, 92038, pers. commun. June 1986.

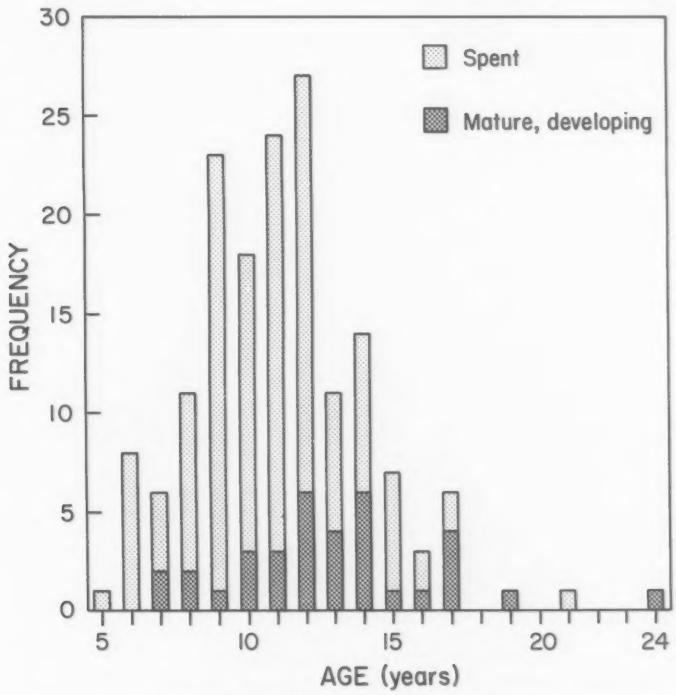

FIGURE 4.—Age-frequency distribution of 162 female Dover sole, classified as either mature with advanced oocytes, or mature and spent.

concerns the small, partially-yolked oocytes (<0.65 mm) that potentially could be recruited to the advanced mode but were excluded from fecundity estimates. Using the average lower limit of advanced oocyte diameters (from only those seven ovaries with clearly separated, advanced modes) as the minimum size of oocytes destined for release, it was assumed that further contribution of smaller oocytes would be unlikely and minimal in the current season.

A compensatory increase in fecundity following a reduction in population density was suggested by Bagenal (1973). We did not detect significant changes in length-specific fecundity for Dover sole despite tripled landings and the suggested decrease in age-specific length since 1977 (Demory et al., fn. 2). However, a decline in reproductive output is unlikely because our data indicate a compensatory shift in size at first maturity. Dover sole now mature at significantly smaller sizes than reported by Harry (1959). We found all fish >320 mm to be mature (the smallest mature fish was 240 mm). Although only 15% (or 245 specimens) of those fish in Harry's study were smaller than 380 mm, they were 330 mm at first maturity, 380 mm when 50% mature, and 420 mm when 100% mature (Fig. 3). Similar sizes at maturity were reported by Hagerman (1952) for Dover sole collected in northern California in 1949. The 45 females (5% of total sample) <330 mm were all immature.

The evident change in size at maturity during the interim 35 years may reflect differences in the criteria used for assessing stage of maturity, and in the time of year and size of the fish used for maturity assessments. Harry collected samples between May and October, which excludes the peak spawning months of December and January. Postspawning, inactive, mature ovaries are difficult to differentiate from immature ones during the early summer months using anatomical or histological criteria (Hunter, fn. 4). Classifying postspawners as immature would lead to a greater size at 50% maturity than that estimated from samples collected within the peak spawning period. Size at first maturity, however, should be relatively independent of season, since it seems unlikely that stage of maturity would be incorrectly identified in all smaller fish. Also, as egg development becomes more evident with the approach of spawning season, the mature ovaries become easier to identify (at least in Harry's August–October samples). Despite these potential problems with data comparisons, a decrease in length at maturity is clear and supported by evidence that Dover sole ≥370 mm collected in the Columbia area during the 1980–81 spawning season were all mature (Demory et al., fn. 2).

We cannot assess possible changes in the age-maturity relationship, because comparable ageing methodology was not used by Harry (1959). It cannot be inferred, however, that Dover sole are maturing at younger ages concurrently with smaller sizes, because length at age has also declined.

Although the decrease in length at maturity implies that individual reproductive potential is improved, lack of historical information on accurate age-specific maturity and fecundity makes it impossible to detect any net change in reproductive output per individual. To identify changes in the reproductive output of the Dover sole off Oregon, a reliable assessment of spawning biomass, size and age structure of the population, and both length and age at maturity is required.

Increased landings and effort may have affected the duration and timing of the spawning season, which could influence year class strength. Size-selective exploitation removes relatively more of the larger and older Dover sole (Best 1961). Larger individuals are not only more fecund, but appear to have a longer and/or later spawning period than small, young fish. The reproductive status and population dynamics of Dover sole, as influenced by factors discussed here, can be further understood with continued, appropriate, long-term research.

Acknowledgments

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Digestive-Gland Histology in Paralarval Squids (Cephalopoda: Loliginidae).

The transition from hatchling to adult in cephalopods does not involve a radical metamorphosis as is found in many other marine invertebrates (Boletzky 1974), but distinctive changes occur early in development (Vecchione 1979, 1981, 1982), similar to those found in fishes. The highest, and perhaps the most variable, rates of prespawning mortality in cephalopods occur during this paralarval development. A recent review of the early life history of cephalopods (Vecchione 1987) presented evidence that starvation, resulting from failure to feed successfully after absorption of the internal yolk, may be a major cause of paralarval mortality. However, other explanations, such as predation or suboptimal environmental conditions, may also explain high paralarval mortality rates. To test among these alternatives, methods must be developed to determine whether paralarval squids are suffering from starvation.

Similar problems exist in ichthyoplankton

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ecology. Histology has been used to determine whether larval fishes are starving at sea (O'Connell 1976, 1980; Theilacker 1978, 1986; Govoni 1980; Eldridge et al. 1981; Kashuba and Matthews 1984). In cephalopods, the digestive gland is uniquely suited to be a target for a histological study of feeding history. The cells of the digestive gland can be categorized along a developmental continuum of immature, synthesizing, mature, and resting cells of a single type (Boucaud-Camou and Yim 1980; Boucaud-Camou and Boucher-Rodoni 1983; Boucher-Rodoni et al. 1987). Boucher-Rodoni et al. (1987) proposed that the developmental condition of the cells of the digestive glands of very young *Sepia officinalis* and other cephalopod paralarvae could be used as an indicator of successful first-feeding.

The digestive-gland cells in the genus *Loligo* undergo a developmental sequence similar to that of other cephalopods (Portmann and Bidder 1928), although Boucher-Rodoni and Boucaud-Camou (in press) have found that the digestive gland in *Loligo* differs substantially from that of other cephalopods. The cells of the loliginid digestive gland are characterized by large apical vacuoles containing lipids and carbohydrates (Bidder 1950, 1966).

We examined the digestive glands of paralarval *Loligo*, both *L. pealei* from field collections and *L. forbesi* that had been hatched and maintained in the laboratory under known nutritional conditions. Specifically, we wanted to see whether the presence of mature digestive-gland cells could be associated with successful first-feeding in the commercially important squid family Loliginidae.

Materials and Methods

Laboratory squids were obtained from an experiment in culturing the eastern Atlantic species *Loligo forbesi* (Hanlon et al. 1985). Because the primary objective of the experiment was to determine methods for successfully culturing squids, the squids could not be sacrificed on an optimum schedule for determination of starvation. Furthermore, because the scope of the feeding experiments was limited, the sample available to us (other investigators were interested in other problems) was quite small.

These squids included hatchlings (<1 d old), some of which had been offered zooplankton as food and some that had been kept without food. Also included were squids >1 wk old. These older squids had survived past the point at which death from starvation normally occurs in unfed squids. Among these older squids were some that had been offered zooplankton as food and some that had been kept without food in a seawater culture medium containing a high concentration (10 mg C per L) of dissolved organic material (DOM). Squids collected in the field were *Loligo pealei* sorted from zooplankton samples from the western North Atlantic. The *L. pealei* were chosen to represent the entire paralarval size range (Vecchione 1981) (Table 1).

TABLE 1.—Paralarval squids examined for digestive-gland histology. DOM = Dissolved Organic Material.

Loligo pealei Dorsal mantle length	*Loligo forbesi* Dorsal mantle length	Age	Treatment
2.0 mm	3.8 mm	<1 day	nonfed
2.0 mm	4.1 mm	<1 day	nonfed
2.6 mm	3.3 mm	<1 day	fed
3.0 mm	3.9 mm	<1 day	fed
3.4 mm	3.4 mm	>1 week	fed
5.1 mm	4.0 mm	>1 week	fed
6.4 mm	4.2 mm	>1 week	DOM
6.9 mm	4.4 mm	>1 week	DOM

The field-collected squids were fixed and preserved in 4% formaldehyde in seawater, whereas those cultured in the laboratory were fixed in Bouin's solution and sectioned shortly after fixation. For all squids, 10 μm horizontal sections were prepared after having been embedded in paraffin. Sections were cleared with oil of wintergreen and stained with hematoxylin and eosin. Observations were standardized by selecting sections that, as much as possible, were ventral to the posterior salivary gland and dorsal to the ink sac, although in some squids these organs overlapped dorsoventrally.

Results

Some mature cells containing conspicuous apical vacuoles were found in all squids. Numbers and sizes of vacoules varied as did the relative volume of the glandular epithelium of the digestive gland.

Hatchlings of *L. forbesi* were all similar in appearance, both nonfed (Fig. 1A) and those that had been offered food and therefore may have fed (Fig. 1B, C). The digestive glands appeared to be robust, with thick glandular epithelium that occupied more volume than the

lumen. Numerous small vacuoles were seen throughout the tissue of both the fed and the nonfed squids. Thus, a large percentage of the cells of squids from both treatments could be considered to be mature. Additionally, a few medium-sized and large vacuoles were found in the nonfed hatchlings (Fig. 1A).

The greatest differences between feeding-treatments were found in the *L. forbesi* that had survived for more than 1 week. The digestive-gland tissue of the squids that had been offered zooplankton, and presumably had fed because of their longevity, consisted of thin walls with many long, thin lamellae that extended into a very large lumen (Fig. 2A, B). The volume of the lumen was much greater than that of the digestive-gland tissue. This tissue was characterized by vacuoles that were few but very large (Fig. 2B). Conversely, the digestive glands of the squids that had been raised on DOM had grown but had retained an overall appearance very similar to that of the hatchlings. Digestive-gland tissue was massive, occupying much more volume than the lumen; furthermore, it was

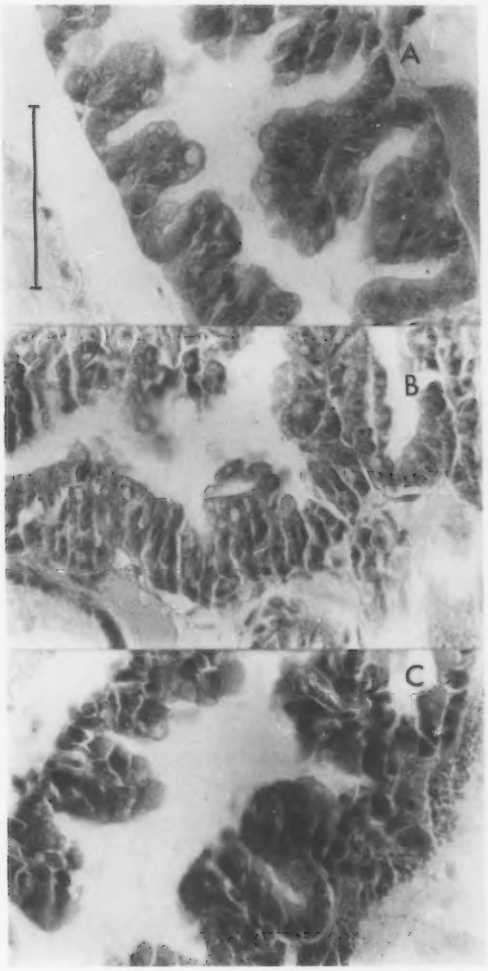

FIGURE 1.—Laboratory-hatched *Loligo forbesi*, < 1 day old: A, 3.8 mm dorsal mantle length (DML), nonfed; B, 3.3 mm DML, from a container with zooplankton food organisms present; C, 3.9 mm DML, from a container with zooplankton food organisms present. Scale bar = 100 μm.

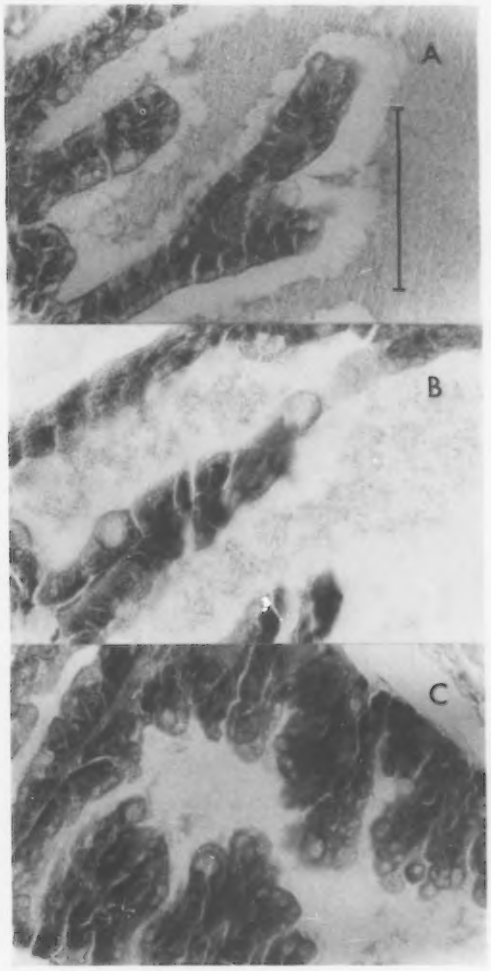

FIGURE 2.—Laboratory-reared *Loligo forbesi*, > 1 week old: A, 3.4 mm dorsal mantle length (DML), fed; B, 4.0 mm DML, fed; C, 4.2 mm DML, from a container with elevated concentrations of dissolved organic matter. Scale bar = 100 μm.

characterized by numerous small to medium-sized vacuoles (Fig. 2C).

Differences between feeding-treatments in the gross morphology of the digestive gland were dramatic (Fig. 3). The digestive glands of squids that had been raised on zooplankton were thin-walled, with large fluid-filled lumina traversed by thin lamellae (Fig. 3A). The digestive glands of squids raised on DOM (Fig. 3B) appeared to be much more robust and well developed, with thick tissue and many small tubules.

Numerous small-to-large vacuoles were found in even the smallest of the field-collected *L. pealei* (Fig. 4A). Digestive-gland tissue was thick, although a large central lumen was present. The internal yolk sac remained in one squid of 2.0 mm dorsal mantle length (DML). In larger *L. pealei* (Fig. 4B, C), vacuoles were numerous and of various sizes but the digestive-gland tissue varied in thickness. In the largest squids examined, tissue growth had filled most of the lumen so that it was characterized by many smaller tubules, similar to those in Figure 4C. These larger paralarvae had few vacuoles but those present were large.

Discussion

Whereas *L. forbesi* has large hatchlings that can be reared in the laboratory (Hanlon et al. 1985), paralarval *L. forbesi* are seldom collected

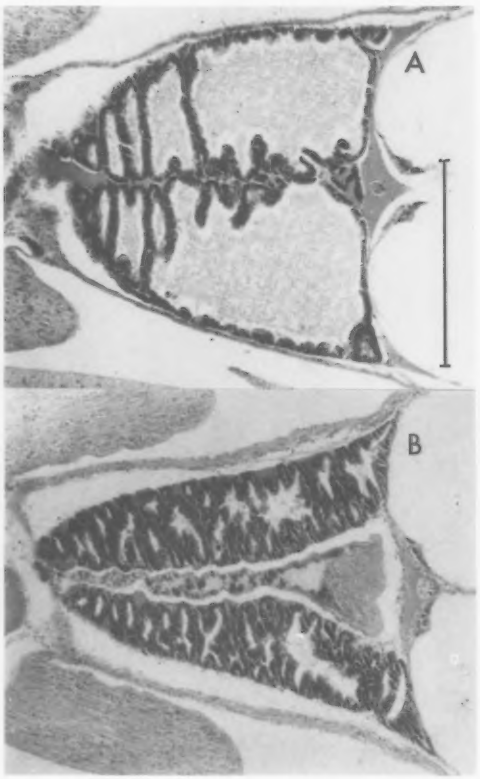

FIGURE 3.—Digestive glands of laboratory-reared *Loligo forbesi*, > 1 week old: A, 4.0 mm DML, from a container with zooplankton food organisms present; B, 4.2 mm DML, from a container with elevated concentrations of dissolved organic matter. Scale bar = 500 μm.

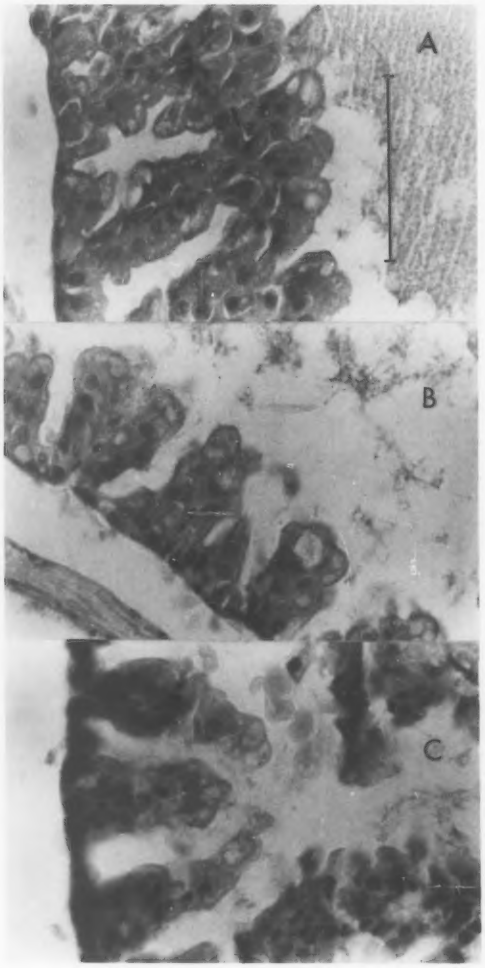

FIGURE 4.—Field-collected *Loligo pealei* paralarvae: A, 2.0 mm dorsal mantle length (DML); B, 3.0 mm DML; C, 3.4 mm DML. Scale bar = 100 μm.

in plankton samples (Holme 1974). *Loligo pealei*, however, is commonly collected in the field (Vecchione 1981), but hatches at a much smaller size and is difficult to rear in the laboratory, suffering at least 99% mortality in the first few days, presumably from starvation (Hanlon et al. 1987). The former species, therefore, was used for laboratory studies and the latter for field observations, even though extrapolation from one species to another must be approached with caution.

The *L. forbesi* hatchlings (< 1 d old) that had not been offered food had unquestionably not fed, but their digestive glands contained many mature cells with conspicuous apical vacuoles. Therefore, the presence or absence of vacuoles is not an adequate indicator of successful first-feeding in this species. Even in *Sepia*, there were indications from tissue-culture experiments that digestive-gland cells may mature slowly in unfed hatchlings (Boucher-Rodoni et al. 1987). Similarly, the large vacuoles cannot be taken as an indication of having fed because the unfed hatchlings had large vacuoles as did the older *L. forbesi* that had been fed and had survived for more than 1 week.

Hatchlings <1 d old that had been offered food may or may not have fed. However, unfed hatchlings typically die, presumably from starvation because the internal yolk sac has been absorbed, within 5 days after hatching. Therefore, the older *L. forbesi* (>1 wk old) that had been offered food probably had fed, although no observations were available to indicate the number of hours or days between their final meal and their time of death and fixation.

Culturing experiments have indicated that elevated concentrations of DOM enhance survival of paralarval *L. forbesi* (P. G. Lee[1]). Thus, the squids from the DOM experiment, while not having fed in the typical sense, had grown and, therefore, were not necessarily starving. The DOM added was a complete diet formulation and would have provided all necessary acids. Approximately 50% of the paralarvae in the DOM experiment survived for 10 days after hatching. Ten of 184 paralarvae from the DOM experiment lived for 12 days, before the experiment was terminated because of an intense bacterial bloom (P. G. Lee[2]). Throughout that period, mortality was higher for paralarvae that had been offered food than for those cultured on elevated DOM.

Digestive-gland structure in the older *L. forbesi* that had been fed was distinctly different from those raised on DOM. Whereas the fed squids had a few very large vacuoles, the DOM squids had very many smaller vacuoles. As noted above, the large vacuoles cannot be taken as an indication of having fed because the unfed hatchlings also had similarly large vacuoles. Furthermore, digestive-gland tissue was very thin on the fed squids compared with those from either the DOM experiment or the field-collected *L. pealei*. It is possible that the fed paralarvae had fed enough to survive beyond yolk absorption but not enough to be completely healthy.

Alternatively, it is possible that the distended lumina and the large vacuoles of the older, fed squids may have been caused by alimentary fluid reaching the digestive gland and entering the cell by phagocytosis for intracellular digestion. If this was the case, the squids raised on DOM simply would have retained immature digestive gland morphology and histology. However, because the field-collected squids, especially the larger ones, were similar in digestive gland structure to those raised on DOM, it seems likely that this is the normal, well-nourished condition. Furthermore, the digestive glands of the field-collected squids and those raised on DOM are both similar in structure to the adult condition (c.f. Boucher-Rodoni and Boucaud-Camou, in press). In the largest field-collected squids, which undoubtedly had passed first feeding successfully, the lumen was largely filled by tissue growth, transforming it into a series of many small tubules. If thin walls of the digestive gland are indicative of poor feeding, none of the field-collected squids showed this indication.

In conclusion, we are not certain which condition (thin tissue with a few large vacuoles or thicker tissue with many smaller vacuoles) is the healthier state. However, we believe that it is likely that the condition of thick tissue with many small vacuoles and reduced lumina, found in the DOM and field-collected squids and similar to the adult condition, represents the healthy, well-nourished condition. The differences in gross morphology between these two conditions are obvious even in cursory examination of sections of the digestive glands of paralarvae. This characteristic may therefore be useful for deter-

[1]P. G. Lee, University of Texas Marine Biomedical Institute, Galveston, TX, pers. commun. 1986.

[2]P. G. Lee, University of Texas Marine Biomedical Institute, Galveston, TX, pers. commun. 1987.

mining the nutritional condition of paralarval loliginids.

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Roger Hanlon and Phillip Lee provided the laboratory-reared squids (culture project supported by the Department of Health and Human Services grant RR01024-11) as well as helpful comments on raising cephalopods. Robert Herschler was kind enough to let M. Vecchione use his microscope for photomicrography. Ruth Gibbons prepared the plates. We appreciate reviews of the manuscript by Eve Boucaud-Camou, Renata Boucher-Rodoni, Roger Hanlon, Katharina Mangold, and Richard Young. Eve Boucaud-Camou kindly sent me several unpublished micrographs, and a copy of her paper which is in press, on the digestive glands of adult *Loligo*. Financial support for this research was provided by National Science Foundation grant OCE-8600541 to M. Vecchione.

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Identification of Habitat of Juvenile Snappers in Hawaii

Deepwater snappers have high commercial and recreational value throughout the tropics, and their fisheries and species biology have been widely studied. However, little is known about the ecology of the juveniles between settlement to the demersal habitat and recruitment to the adult population (Munro 1987). In Hawaii, no information regarding location, size, or habitat of juvenile lutjanids has emerged after more than a decade of concentrated studies of adult stocks (Ralston 1980; Humphreys 1986). The absence of observations and collections of juvenile lutjanids or of their occurrence as prey items in the adult habitat suggests that they settle elsewhere prior to recruitment.

Adult snappers have been frequently reported as being associated with structural relief at depths of 100–500 m (Parrish 1987). In contrast, juveniles have not been caught or visually observed in such habitats in surveys made with scuba or submersible vehicles (Ralston et al. 1986; Moffitt et al. 1989). Owing to the lack of conventional scientific evidence about the habitat of juveniles, occasional reports of juveniles captured by shallow-water recreational fishermen in Hawaii continued to go largely unnoticed by researchers until one angler brought back live juvenile specimens of both *Pristipomoides filamentosus* and *Aprion virescens* in September 1988. This tangible evidence provided the stimulus to conduct some exploratory fishing in relatively shallow waters and to attempt to visually observe the fishes' habitat. This report summarizes the results of that investigation.

Methods

During October 1988, the bottom was fished and observed with scuba at three stations off the eastern side of the Hawaiian Island of Oahu. Stations 1 and 2, separated by 2 km along the coast, were situated outside the barrier reef and between the two main entrance channels of Kaneohe Bay; station 3 was located southeast of Mokapu Peninsula in Kailua Bay (Fig. 1). Most fishing was done in midmorning (0800–1200). At station 3, one afternoon and evening sampling was taken in addition to the morning sampling.

A single day of intensive fishing was done at each station from a small boat with two lines, each bearing three No. 10 circle hooks baited with live shrimp. Fishing was limited to depths of 31–76 m, to allow observation of habitat by scuba. At each station, the boat drifted or occupied sequential, anchored positions along a transect across the bottom contours while the fishing lines were bounced off the bottom. The depth was measured periodically during fishing and immediately following the landing of juvenile bottom fishes.

Habitat observations with scuba were performed at the three stations on mornings soon after the sampling was completed, at the locations and depths where target species had been caught earlier. Fishing with a single line helped confirm observation locations on two occasions: target species were landed immediately before or during the dive. At least two dives were made at each station, one or more in shallow (40–50 m) and the other in deep (51–76 m) water. At stations yielding no fish in either depth range, observations were conducted at depths similar to those yielding fish at the other stations. With the exception of the 52 m dive at station 2, dives in the deep ends of the transects occurred at what proved to be the most productive fishing depths (>61 m). Restricted bottom time at these depths limited diving activities to observing habitat and scanning an area of about 6,000 m^2 for target species.

Additional specimens were concurrently collected from waters off Lahilahi Point on western Oahu by the same methods, except that artificial bait was used on a single line and depth was only estimated (60–90 m) by the amount of line deployed. Stomachs and hindguts of *P. filamentosus* from all sources were examined, and prey items were counted and roughly classified. The *P. filamentosus* containing food items were used in the analysis of occurrence (prey type as a percentage of all individuals eaten) and frequency (percentage of fish containing each prey type).

Results and Discussion

A total of 36 juvenile lutjanids were collected from the three stations (Table 1). *Pristipomoides filamentosus* (n = 30) were caught at all three stations, all at 61–73 m depths; 25 were captured at station 1. Five *Aprion virescens* and the one *Aphareus rutilans* were taken at station 2 at 40 m. At stations 1 and 2, the catch rate consistently declined at all depths in the late morning hours. At station 3, no fish were caught until dusk, when four *P. filamentosus* were

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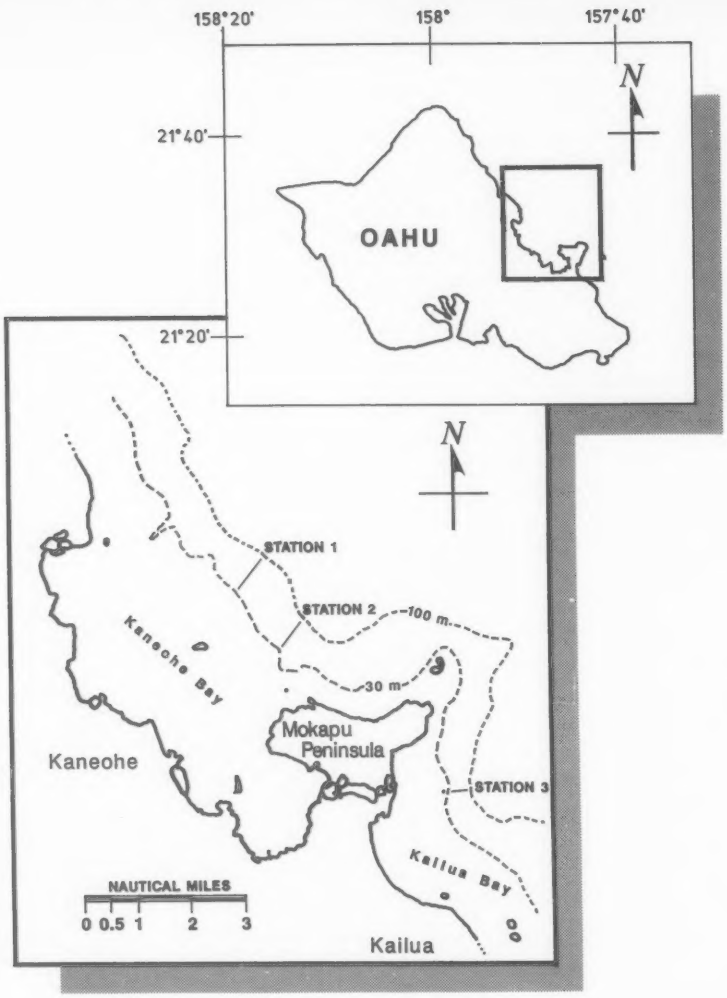

FIGURE 1.—Locations of the three established east Oahu stations.

taken. The west Oahu site yielded seven more *P. filamentosus* for analysis. These results suggest a possible minimum depth of about 61 m for juvenile *P. filamentosus* at the sampled sites.

The scuba observations indicated that the habitat was generally similar at all three stations, but the substrate within each station varied with depth. At the shallow end, the bottom was hard, flat, and devoid of vertical relief. A thin veneer of sand was present, with stands of live *Halimeda* algae evenly distributed over the bottom. Infrequent, shallow depressions in the bottom provided the only substantial relief in which newly settled reef fish (e.g., Pomacentridae and Labridae) were aggregated. No juvenile lutjanids were sighted at this shallow habitat at any of the three stations, although during observation of the habitat at station 2, two *Aprion virescens* were hooked.

The bottom habitats observed at the deep ends of stations 1 and 3, where nearly all the *Pristipomoides filamentosus* were caught, were also similar. The bottom was flat and almost completely devoid of any relief other than minor features produced by sparse benthic biota. The substrate consisted entirely of soft, deep sediment heavily penetrated by burrowing invertebrates. Although no fish were seen during these deep dives, their presence was established at station 1 by the capture of a single *P. filamen-*

TABLE 1.—Results from sampling at three stations on the eastern side of Oahu and at a supplementary site off west Oahu. Numbers in parentheses indicate the actual dive depths (in meters).

Species caught	Depth (m)	Bottom substrate by depth range	
		40–50 m	51–76 m
Station 1			
25 *Pristipomoides filamentosus*	61–73	Hard, flat, with *Halimeda* algae (43)	Flat, soft, fine sediment with invertebrate burrows (69)
Station 2			
5 *Aprion virescens*	40	Hard, flat, with *Halimeda* algae (40)	Flat, coarse sand, without fine sediment (52)
1 *Aphareus rutilans*	40		
1 *P. filamentosus*	67		
Station 3			
4 *P. filamentosus*	67	Hard, flat, without *Halimeda* algae (43)	Flat, soft, fine sediment with invertebrate burrows (70)
West Oahu			
7 *P. filamentosus*	>61		
1 *Aprion virescens*	>61		

tosus at anchor just prior to the dive. At station 2, a somewhat shallower (52 m) dive revealed a substrate consisting entirely of soft *Halimeda* sand without invertebrate burrows or visible fine sediment. After the bottom observations, additional fishing at >61 m depths yielded a single *P. filamentosus*.

Since the density of juvenile lutjanids was probably not great at any location, it is not surprising that they were never sighted by divers. Avoidance behavior by the juveniles may have contributed to the lack of sightings. Our impressions of the habitat based on dive observations were consistent with those from other surveys of the study area (Smith et al. 1973; Coulbourn et al. 1988).

The portion of the life cycle during which juveniles occupy the observed habitat remains unknown. Fork lengths (FL's) of the collected *P. filamentosus* (n = 32) ranged from 10.1 to 20.7 cm; most individuals were clumped at the low end of the range. Planktonic individuals as large as 5 cm have been recorded for a somewhat smaller species, *P. sieboldii*, by Leis (1987). Until the present study, the smallest recorded *P. filamentosus* was 18 cm FL, caught by handline during sampling for adults (Ralston 1981). Using Ralston and Miyamoto's (1983) estimated growth curve derived from adult specimens, a fish of 18 cm FL would be approximately 1 yr old.

Larger identifiable prey items recovered from the stomachs of 22 juvenile specimens of *P. filamentosus* included early juvenile fish (probably recently settled) and cephalopods (including an octopod) (Table 2). The hindgut contained small planktonic crustaceans, appendicularians, and other gelatinous plankton. Most prey individuals were small, but the general taxonomic composition of the diet of the juveniles did not appear greatly different from that of adults. Crustaceans and salps commonly occur in the diet of adult *P. filamentosus* (Kami 1973; Parrish 1987).

TABLE 2.—Approximate percentage of number and frequency of identifiable prey items found in *Pristipomoides filamentosus* juveniles (n = 22).

Prey type	Percent occurrence	Percent frequency
Juvenile fish	2	18
Fish scale	3	18
Small crustaceans	90	72
Cephalopods	2	9
Gelatinous plankton	3	18

Relatively flat, soft bottoms such as occur at these stations have been largely ignored as potentially important habitat for these deepwater lutjanids, but they may provide essential habitat for the juveniles. Artificial structures placed in depths of 61–117 m in Hawaii successfully aggregated deepwater lutjanid adults, but

failed completely to attract juveniles (Moffitt et al. 1989). Although there is little evidence that juveniles avoid such high relief features, there is no evidence of positive association. The limited gut samples from our juveniles did not indicate any material endemic to hard substrate (e.g., coral; obligate, hard bottom-associated invertebrates). Association with structural relief or even with adult bottom fish may put juveniles at risk (Johannes 1978). For example, predators may routinely visit high structural features. Thus, juveniles may pass their early settled life on flat, soft, featureless bottoms. The use of special habitats by prerecruits to avoid competition and possible predation has been observed in both temperate (Carlson and Haight 1976) and tropical fishes (Shapiro 1987). Juvenile lutjanids may also occur on hard, flat bottoms with some limited degree of relief. No fishing on such bottoms was attempted, and extensive sampling effort would be required to eliminate the possibility that such habitat is used.

This brief, preliminary investigation has demonstrated only the presence of juveniles of recreationally and commercially important lutjanids in habitat relatively close to the fishing grounds for adults, but not where adults congregate. The boundaries of that habitat and the characteristics that make it attractive to juveniles remain to be defined. Some basic attributes, such as depth, temperature, substrate, and the general nature of bottom relief, are relatively easy to measure and describe for large areas. Characterization of the habitats used by juvenile lutjanids will improve the ability to assess and manage productive substrate. Ichthyoplankton sampling has yielded relatively few specimens of larval lutjanids (Collins et al. 1980; Leis 1987), and the value of that approach for assessing adult stocks seems limited. A focused program of sampling and monitoring the juvenile population and estimating the available habitat suitable for them may provide more effective indicators of potential recruitment and indicate the prospects for future adult stocks.

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NOAA Technical Reports NMFS published during the first 6 months of 1989.

72. Age determination methods for northwest Atlantic species. By Judy Penttila and Louise M. Dery (editors). December 1988, iv + 135 p., 2 app.

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Atlantic herring, *Clupea harengus*. By Louise M. Dery. Pages 17–22, 12 figs.

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Surf clam, *Spisula sollidissima*. By John W. Ropes and Gary R. Shepherd. Pages 125–128, 3 figs.

Ocean quahog, *Arctica islandica*. By John W. Ropes. Pages 129–132, 3 figs.

73. Marine flora and fauna of the eastern United States. Mollusca: Cephalopoda. By Michael Vecchione,

Clyde F. E. Roper, and Michael J. Sweeney. February 1989, iii + 23 p., 29 figs.

74. Proximate composition and fatty acid land cholesterol content of 22 species of northwest Atlantic finfish. By Judith Krzynowek, Jenny Murphy, Richard S. Maney, and Laurie J. Panunzio. May 1989, iii + 35 p., 3 tables, 1 app.

75. Codend selection of winter flounder, *Pseudopleuronectes americanus*. By David G. Simpson. March 1989, iii + 10 p., 5 figs., 5 tables.

76. Analysis of fish diversion efficiency and survivorship in the fish return system at San Onofre Nuclear Generating Station. By Milton S. Love, Meenu Sandhu, Jeffrey Stein, Kevin T. Herbinson, Robert H. Moore, Michael Mullin, and John S. Stephens, Jr. April 1989, iii + 16 p., 14 figs., 3 tables, 4 app.

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